



EFFECTS OF EXPERIMENTAL COWBIRD REMOVALS ON BROOD PARASITISM AND NEST PREDATION IN A GRASSLAND SONGBIRD

BRETT K. SANDERCOCK,¹ ERIN L. HEWETT,² AND KARL L. KOSCIUCH³

Division of Biology, 116 Ackert Hall, Kansas State University, Manhattan, Kansas 66506, USA

ABSTRACT.—Brood parasitism and predation are two factors that limit seasonal fecundity in grassland songbirds. We removed Brown-headed Cowbirds (*Molothrus ater*) in a switchback experiment to examine the effects of brood parasitism and nest predation on the productivity of Dickcissels (*Spiza americana*). Nesting Dickcissels were monitored at four study plots in northeast Kansas in a two-year study. Brown-headed Cowbirds were captured with drop-in traps at two removal plots, two unmanipulated plots were reference plots, and treatments were reversed between years. To evaluate the effect of Brown-headed Cowbird removals, we compared the percentage of nests parasitized, rates of multiple parasitism, clutch size, daily nest survival rates, and overall productivity per nest between removal and reference plots. Removals of Brown-headed Cowbirds successfully reduced the probability of parasitism and rates of multiple parasitism, but only in one of two years. Brown-headed Cowbirds did not appear to contribute to nest losses, given that few nests were abandoned because of cowbird activity and that the probabilities of nest parasitism and nest survival declined simultaneously over the breeding season. Overall, nest productivity showed no difference between treatments in either year, despite reduced rates of parasitism at removal plots in 2004. High rates of nest predation minimized the potential benefits of Brown-headed Cowbird removals for increasing productivity of Dickcissels. Our results demonstrate that removals can reduce parasitism levels but that the success of removal programs may vary annually, particularly in regions where Brown-headed Cowbirds and nest predators are abundant. Management actions that minimize parasitism and predation by modifying habitat structure may provide better alternatives to programs based on removals. Received 5 August 2006, accepted 25 February 2008.

Key words: Brown-headed Cowbird, Dickcissel, fecundity, management, *Molothrus ater*, productivity, *Spiza americana*.

Efectos de la Remoción Experimental de *Molothrus ater* sobre el Parasitismo de Nidada y la Depredación de Nidos en un Ave Canora de Pastizal

RESUMEN.—El parasitismo y la depredación de la nidada son dos factores que limitan la fecundidad estacional en las aves canoras de pastizal. Removimos individuos de *Molothrus ater* para examinar experimentalmente los efectos del parasitismo de la nidada y de la depredación de nidos sobre la productividad de *Spiza americana*. Monitoreamos individuos de *S. americana* que estaban anidando en cuatro parcelas de estudio en el noreste de Kansas durante dos años. Los individuos de *M. ater* fueron capturados con trampas en dos parcelas de remoción y dos parcelas no manipuladas sirvieron de referencia; los tratamientos fueron revertidos entre los años. Para evaluar el efecto de la remoción de *M. ater*, comparamos el porcentaje de nidos parasitados, las tasas de parasitismo múltiple, el tamaño de la nidada, las tasas de supervivencia diaria de los nidos y la productividad total por nido entre las parcelas de remoción y las de referencia. La remoción de *M. ater* redujo con éxito la probabilidad de parasitismo y las tasas de parasitismo múltiple, pero sólo en uno de los dos años. Esta especie de parásito no pareció contribuir a las pérdidas de nidos, dado que pocos nidos fueron abandonados como consecuencia de su actividad y a que las probabilidades de parasitismo y de supervivencia de los nidos disminuyeron a lo largo de la estación reproductiva. En total, la productividad de los nidos no mostró diferencias entre los tratamientos en ninguno de los años, a pesar de las tasas reducidas de parasitismo en las parcelas de remoción observadas en 2004. Las altas tasas de depredación de nidos minimizaron los beneficios potenciales de la remoción de *M. ater*, que apuntaban a incrementar la productividad de *S. americana*. Nuestros resultados demostraron que la remoción puede reducir los niveles de parasitismo, pero que el éxito de los programas de remoción puede variar anualmente, particularmente en las regiones donde *M. ater* y los depredadores de nidos son abundantes. Las acciones de manejo que minimizan el parasitismo y la depredación mediante la modificación de la estructura del hábitat pueden brindar mejores alternativas que los programas basados en la remoción.

¹E-mail: bsanderc@ksu.edu

²Present address: Department of Biological Sciences, Virginia Polytechnic Institute and State University, 2125 Derring Hall, Blacksburg, Virginia 24061, USA.

³Present address: Tetra Tech EC, 1750 SW Harbor Way, Portland, Oregon 97201, USA.

GRASSLAND BIRDS ARE OF conservation concern because long-term monitoring programs have shown that population declines are widespread and ongoing (Murphy 2003). Major causes of population declines among species that breed in temperate grasslands include widespread loss and fragmentation of breeding habitat (Winter and Faaborg 1999, Brennan and Kuvlesky 2005), effects of rangeland management on habitat structure (Robbins et al. 2002, Patten et al. 2006, Powell 2006), and events at wintering sites (Basili and Temple 1999). Effective management of grassland birds requires a better understanding of (1) the demographic parameters that have the greatest influence on population viability and (2) the effects of environmental factors on population demography (Citta and Mills 1999, McCoy et al. 1999, Fletcher et al. 2006).

Two factors that limit the seasonal fecundity of songbirds in North America are brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds") and losses of eggs and young to nest predators. Female cowbirds reduce productivity of songbirds by removing or damaging host eggs in association with parasitic egg laying and may destroy complete nests to induce renesting, thus gaining additional opportunities for parasitism (Granfors et al. 2001, Peer 2006). The presence of parasitic offspring affects host productivity by reducing hatching success of host eggs and by competitive interactions between host and parasitic young (Lichtenstein and Sealy 1998, Zanette et al. 2005). Destruction of nests by predators is also a major cause of reproductive loss among grassland songbirds (Davis and Sealy 2000, Herkert et al. 2003). The effects of parasitism and predation are challenging to disentangle for several reasons: mortality of young from cowbird activity can resemble losses to natural predators, parasitism may facilitate detection of nests by predators, and vulnerability of nests to parasitism and predation may covary as a function of nest placement or parental defense behavior (Arcese et al. 1996, Dearborn 1999, McLaren and Sealy 2000, Zanette et al. 2007). Nevertheless, the effects of brood parasitism are greater than those of losses to nest predation in some songbirds (Woodworth 1999, Ward and Smith 2000, Smith et al. 2002, Hoover 2003), whereas the opposite is true for other species (Rogers et al. 1997, Schmidt and Whelan 1999, Whitehead et al. 2000, Ortega and Ortega 2001).

Experimental manipulation of cowbird abundance is one of the best approaches for investigating the relative effects of parasitism and predation on songbird fecundity (Smith et al. 2002). Understanding the relative importance of these two factors is particularly relevant to applied ecology, because cowbird removals are an integral part of management for songbirds of conservation concern (Robinson et al. 1995, Rothstein and Peer 2005). However, logistical considerations may constrain the experimental design of cowbird removal programs for threatened and endangered species. In some cases, data on host reproduction before cowbird trapping may be available, but spatial and temporal variation in parasitism and predation may be difficult to evaluate if unmanipulated reference plots are not established (Braden et al. 1997, Whitfield et al. 1999, DeCapita 2000). Similarly, the effects of cowbird removals alone can be difficult to evaluate if cowbird trapping is combined with other interventions such as adding of cowbird eggs, removal of cowbird young, or changes in rangeland management (Morrison and Averill-Murray 2002, Kostecke et al. 2005, Kus and Whitfield 2005). Cowbird removal experiments for non-endangered songbirds offer greater flexibility for

experimental design, including opportunities for replication of removal and reference plots (Stutchbury 1997, Smith et al. 2002, Kosciuch and Sandercock 2008).

We combined experimental cowbird removals and intensive nest monitoring to examine the effects of cowbird parasitism and nest predation on the nest productivity of Dickcissels (*Spiza americana*) and Bell's Vireos (*Vireo bellii*; hereafter "vireo"). Dickcissels are migratory songbirds that breed in temperate grasslands of North America and winter in South America (Basili and Temple 1999, Herkert et al. 2003). Dickcissels are a preferred host of cowbirds, and parasitism rates can be high (80–95%) because Dickcissels routinely accept parasitic eggs (Elliott 1978, Peer et al. 2000, Jensen and Cully 2005b, Powell 2006). Vireos are also a preferred host but are parasitized at somewhat lower rates (70–85%), possibly because vireos are shrub-nesters or because they desert parasitized nests (Parker 1999, Kosciuch et al. 2006). Both songbirds are designated as "watch list species of continental importance" by Partners in Flight (Rich et al. 2004). The objectives of the present study were (1) to determine the effects of parasitism and predation on the productivity of Dickcissels, (2) to test the efficacy of cowbird removals as a potential management tool for improving productivity of Dickcissels, and (3) to contrast the demographic effects of cowbird removals on Dickcissels with our previous work on vireos (Kosciuch and Sandercock 2008).

METHODS

Field site.—Our study was conducted from May to July in 2004 and 2005 at Konza Prairie Biological Station in the Flint Hills region of northeast Kansas (39°05'N, 96°35'W). The northern Flint Hills region is characterized by large, unfragmented tracts of tall-grass prairie, rangeland management that combines cattle grazing with prescribed fire, and high densities of cowbirds (Robbins et al. 2002, Jensen and Cully 2005b, Powell 2006). Konza Prairie is a 3,487-ha tallgrass prairie preserve and a core research site in the Long-term Ecological Research (LTER) program of the National Science Foundation. The station is subdivided into ~60 experimental units, and each unit is managed with a different combination of prescribed fire (since 1981, burned, usually in April, at intervals of 1, 2, 4, 10, or 20 years) and rangeland management (since 1987, ungrazed or grazed by domestic cattle [*Bos taurus*] or American Bison [*Bos bison*]). Dickcissels, cowbirds, and vireos are the first, second, and fifth most abundant songbird species at Konza Prairie (Powell 2006).

Male Dickcissels arrive at Konza Prairie and begin to establish breeding territories in early May. Females arrive after territories are established and begin nesting in late May. Dickcissels use a range of different grassland habitats, though densities of birds may be reduced in areas that are burned annually (Hughes et al. 1999, Powell 2006). Females construct open-cup nests in low-lying forbs and grasses, and modal clutch size is four eggs (Zimmerman 1982, Winter 1999). Eggs are laid one per day, incubation begins with the laying of the penultimate egg and lasts 12–14 days, and brood rearing begins at hatching and lasts 8–10 days (Gross 1921, Long et al. 1965, Zimmerman 1982, E. L. Hewett unpubl. data). Nestlings remain near the nest and are fed by the female for about two to three weeks after fledging (Berkeley et al. 2007, Suedkamp Wells et al. 2007). For our calculations of nest survival, we estimated that

the average duration of the nesting cycle of Dickcissels was 24 days (2 days of egg laying + 13 days of incubation + 9 days of brood rearing). To examine seasonal variation in frequency and intensity of parasitism, we estimated the date of clutch initiation for each nest (accuracy ± 2 –3 days) by back-dating from the onset of incubation, date of hatching, or size-classes of nestlings (E. L. Hewett unpubl. data). We divided the breeding season into 11 one-week periods, where week 1 was 16–22 May. The same weekly periods were used in analyses for both years. Female Dickcissels will renest after nest failure but are normally single-brooded in a breeding season (Zimmerman 1982, Walk et al. 2004, Fletcher et al. 2006).

Experimental procedures.—We selected four experimental units at Konza Prairie with extensive encroachment of woody shrubs and high nesting densities of vireos and studied the nesting ecology of Dickcissels and vireos breeding within the boundaries of these study plots. The units were 24–36 ha in size, matched by habitat type and management regime, and ≥ 2 km apart (Fig. 1). Study plots were ungrazed but were ≤ 0.5 km from foraging areas within the bison enclosure, and female cowbirds could commute short distances between foraging and nesting territories (Goguen and Mathews 2001, Kostecke et al. 2003). Each year, we conducted cowbird removals at a subset of plots in a switchback experiment. In 2004, cowbird removals were conducted at two of three plots: 20B and 20C were removal treatments, and K4B was an unmanipulated reference plot. To increase our sample of reference nests in 2004, we also monitored 15 Dickcissel nests in nine other plots that were ≥ 2 km from removal treatments. In 2005, we reversed our treatments and conducted cowbird removals at two of four plots: K4B and 10A/B combined were removal treatments, and 20B and 20C were reference plots.

To capture and remove cowbirds, we deployed three large wooden drop-in cowbird traps ($1.8 \times 1.5 \times 1.8$ m) at the perimeter of each removal plot, at a density of one trap per 11 ha. Each cowbird trap was initially stocked with two or three live decoy birds. Food, water, and shade were provided 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 hand-held nets and euthanized by cervical dislocation when traps contained >20 individuals. We started cowbird removals in the first week of May, which was about three weeks

before Dickcissels began nesting. We operated the traps until mid-July (~ 70 trap days), when dissection of female cowbirds indicated that the ovaries no longer contained developing follicles and egg laying had ceased.

We located Dickcissel nests by observing adult behavior, such as birds carrying nesting material or food, by flushing of incubating females while we traversed study plots, and by discovery of active but unattended nests. To minimize observer effects on nest survival, we marked nest locations in relation to natural features of the environment or by placing a small blue flag ≥ 20 m from the nest site, and by recording distance and bearing to the nest site. Nests were monitored every three or four days and were visited midday during hot, dry conditions to minimize scent trails near nests.

Demographic parameters.—To determine the effects of cowbird removals on the productivity of hosts and brood parasites, we compared six demographic parameters between removal and reference plots: host clutch size, percentage of nests parasitized, rates of multiple parasitism, daily nest survival rates, fledging rates, and overall productivity per nest. We discarded nests if they were discovered during nest construction but never received host or cowbird eggs. We considered nests to be parasitized if they contained one or more cowbird young, and unparasitized if they contained only Dickcissel young. Eggs and nestlings of the host and parasitic young were readily distinguished by coloration. Dickcissel eggs are immaculate blue, whereas cowbird eggs are grayish-brown with dark speckling. Similarly, the rectal flanges in the mouthparts of nestlings were yellow in Dickcissels but white in cowbirds. To determine the clutch size of Dickcissels, we restricted our sample to nests found during incubation and used the maximum count of host eggs observed during all visits to a nest. Our estimate of clutch size may be lower than the total number of eggs laid by the female if host eggs were removed before we discovered the nest. To estimate rates of multiple parasitism, we used the maximum count of parasitic eggs. Multiple parasitism can be caused by one female cowbird parasitizing a host nest with multiple eggs or by different individuals laying eggs jointly (McLaren et al. 2003).

We considered nests unsuccessful if eggs were abandoned in the nest, if signs of predator activity were present (e.g., broken eggs, dislodged nesting material), or if the nest contents disappeared before the estimated date of fledging. Parents at depredated nests were rarely aggressive, and renesting attempts usually began shortly after the failure of the first nest. We considered nests successful if they fledged at least one cowbird or host nestling. Nests were considered to have successfully fledged young if fledglings were seen after departure near the empty nest or if the fledglings were five to eight days old at the last nest visit and parents were later observed to be aggressive in defense of young near the nest. We calculated the number of fledglings per successful nest by the number of young that were present on the last nest visit before fledging. If a nest survived incubation and was successful, we calculated fledging rates as the number of fledglings produced per egg. Fledging rates <1 were attributable to partial nest predation, infertile eggs, damaged eggs that failed to hatch, and mortality of chicks and were calculated separately for Dickcissel and cowbird young.

Statistical analyses.—Statistical analyses of demographic parameters were conducted with SAS (SAS Institute, Cary, North Carolina). As a starting point, we tested for plot-level differences

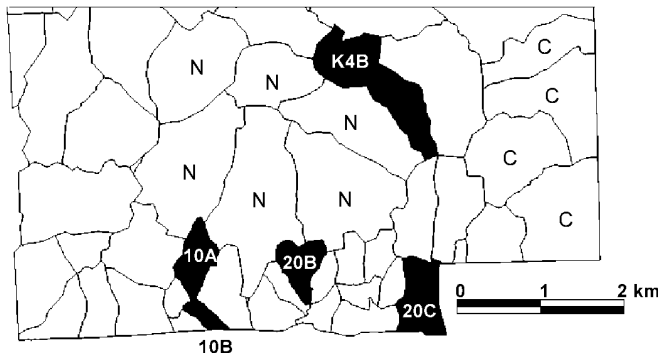


FIG. 1. Location of study plots at Konza Prairie Biological Station, Kansas. Cowbird removals were conducted at 20B and 20C in 2004, and at K4B and 10A/B in 2005. Study plots were ungrazed but were close to sites grazed by native bison (N) or domestic cattle (C).

within each combination of treatment and year. Replicate plots did not differ in the percentage of nests parasitized, in the number of cowbird eggs received per parasitized nest, or in the clutch size of Dickcissels (results not shown). We pooled study plots within treatments by year in subsequent analyses.

We modeled the probability of parasitism as a function of experimental treatment and week of clutch initiation with logistic regression (Proc Genmod in SAS). We included week in our model because seasonal variation in brood parasitism has been reported for Dickcissels (Zimmerman 1983). We used Hosmer-Lemeshow tests to examine goodness-of-fit of the global model (Proc Logistic). Slope coefficients (β) from logistic regression models described the direction of effects, and we used odds ratios (e^β) to calculate the magnitude of the effect size. Odds ratios are widely used in logistic regression but can be misinterpreted because they are not equivalent to the probability of an event (Lloyd and Martin 2005). We tested for seasonal variation in multiple parasitism and Dickcissel clutch size by modeling number of eggs as a function of week of clutch initiation with linear regression (Proc Glim). Next, we modeled the effects of year and treatment on number of eggs with linear models for categorical data (Proc Catmod). We compared fledging rates of Dickcissels and cowbirds with a two-sample t -test (Proc Ttest). All tests were two-tailed, based on Type III likelihood ratio tests or sums of squares, and considered significant at $\alpha \leq 0.05$. We dropped nonsignificant interactions from factorial models and used main-effects models when appropriate.

To estimate daily survival rates (S_d) of Dickcissel nests, we used the nest-survival procedure in MARK (G. C. White, Colorado State University, Ft. Collins, Colorado). Four input variables were included in encounter histories for each nest: the date that the nest was discovered (k), the last date that the nest was still active (l), the date that the nest fate was determined (m), and the fate of the nest (f). We included two factors in our candidate models for nest survival. First, nests were blocked into four groups for each combination of year (2004, 2005) and treatment (removal, reference). Second, we modeled S_d as a linear effect of season to test for possible seasonal trends in nest survival (Zimmerman 1984). All models were constructed with logit link function and the design matrix procedure of MARK, and the number of parameters (K) in each model was set equal to the number of columns in the design matrix. In most mark-recapture models, a first step is to adjust for any lack of fit of the global model to the encounter histories by calculation of a variance inflation factor (\hat{c}). Adjustments are not possible for the nest survival model because the global models are saturated and c is not identifiable (Dinsmore et al. 2002). Model selection was based on Akaike's information criterion values corrected for small sample size (AIC_c). Candidate models were considered in relation to the minimum AIC_c model, and models with ΔAIC_c values ≤ 2 were considered parsimonious. We used ratios of Akaike weights (w_i/w_j) to determine the relative support for different models in our candidate set.

Dickcissel nests were discovered at different stages of the nesting cycle. To obtain an unbiased estimate of productivity per nest (P_n) that controlled for variation in nest exposure, we calculated the mean number of fledglings produced per host nest by $\hat{P}_n = CS \times S_d^{dur} \times FPE$ where CS = clutch size, S_d = daily nest survival rate, dur = duration of a nesting attempt from laying of

the first egg to fledging of the brood (24 days), and FPE = number of fledglings produced per egg. We calculated \hat{P}_n separately for Dickcissels and cowbirds in the two years of the study because CS , S_d , and FPE varied among species and years. To obtain confidence intervals of \hat{P}_n for each of the four combinations of species and year, we used parametric bootstrapping ($n = 5,000$ replicates) in MATLAB, version 6.1 (Mathworks, Natick, Massachusetts). To model CS , we took a draw from a uniform distribution bounded 0 to 1, compared the draw with the observed cumulative frequency distribution for clutch size, and converted it to a draw for number of eggs. For example, if 30% of nests contained three eggs, 40% contained four eggs, and all others contained five eggs, draws from a uniform distribution in the ranges of 0 to 0.3, >0.3 to 0.7, and >0.7 would be converted to draws of 3, 4, and 5 eggs, respectively. We modeled S_d and FPE as draws from beta distributions to bound probabilities within the range 0 to 1. To compensate for slight discrepancies between the mean estimates and means of the bootstrap distributions, we calculated bias-corrected 95% confidence intervals (CI) = $\Phi [2 \Phi^{-1}(F) \pm 1.96]$, where Φ = the normal cumulative distribution, Φ^{-1} is the inverse normal cumulative distribution, F is the fraction of bootstrap values smaller than the estimate of mean productivity per nest (~ 0.5), and 1.96 is the critical value for 95% CI. We tested for differences in nest productivity between the removal and reference plots by selecting pairs of values from the bootstrap distributions at random, by calculating a distribution of differences (removal minus reference), and by calculating the P value as the fraction of difference values greater than or equal to the observed difference in mean productivity (Gotelli and Ellison 2004).

RESULTS

In 2004, we removed 76 adult female, 231 adult male, and 39 juvenile cowbirds ($n = 346$) from plots 20B and 20C between 7 May and 14 July. In 2005, we removed 95 adult female, 493 adult male, and 46 juvenile cowbirds ($n = 634$) from plots 10A/B and K4B between 3 May and 14 July. We had no incidental mortality among nontarget bird species. The first male Dickcissels arrived on 7–8 May and the first Dickcissel nests were discovered on 27 May in both years. We found 53 and 27 Dickcissel nests at removal and reference plots in 2004 ($n = 80$), and 45 and 44 nests at removal and reference plots in 2005 ($n = 89$), respectively.

Probability of parasitism.—The percentage of nests parasitized was greater at reference plots than at cowbird removal plots in 2004 (85% vs. 51%, $\chi^2 = 8.9$, $df = 1$, $P = 0.003$, odds ratio = 5.5, 95% CI: 1.7–18.2; Table 1). In 2005, the percentage of nests parasitized was similar at both reference (82%) and removal plots (78%, $\chi^2 = 0.3$, $df = 1$, $P = 0.60$, odds ratio = 1.3, 95% CI: 0.5–3.7). Thus, we blocked by year to model seasonal variation in the probability of parasitism.

Goodness-of-fit tests showed that the global logistic regression model with the effects of treatment, week of clutch initiation, and an interaction term was a good fit to the data in 2004 (Hosmer and Lemeshow test, $\chi^2 = 4.6$, $df = 6$, $P = 0.59$) and 2005 ($\chi^2 = 12.2$, $df = 6$, $P = 0.06$). The interaction between treatment and week was not significant in either 2004 ($\chi^2 = 0.07$, $df = 1$, $P = 0.78$) or 2005 ($\chi^2 = 0.90$, $df = 1$, $P = 0.65$), so we used models with main effects only for parameter estimation. In 2004, the probability of parasitism differed between treatments ($\chi^2 = 10.1$, $df = 1$, $P = 0.002$)

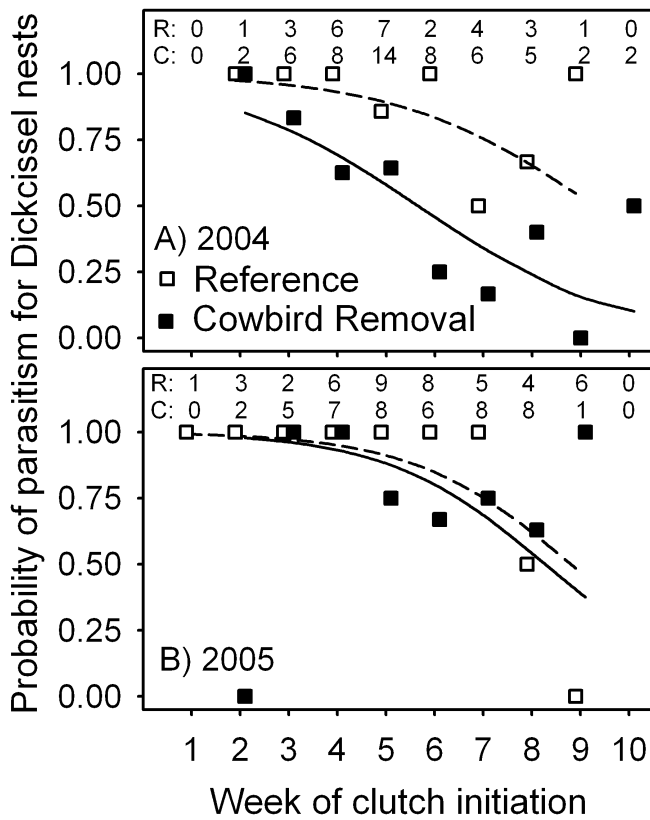


FIG. 2. Probability of brood parasitism for Dickcissels in (A) 2004 and (B) 2005 at reference plots (2004, $n = 27$ nests; 2005, $n = 44$ nests) and cowbird removal plots (2004, $n = 53$ nests; 2005: $n = 45$ nests) at Konza Prairie Biological Station, Kansas. Seasonal variation in the probability of brood parasitism was modeled with logistic regression for reference plots (open squares, dashed lines) and cowbird removal plots (filled squares, solid lines). Sample size of nests in reference plots (R) and cowbird removal plots (C) are given at the top of each panel. Week 1 = 16–22 May.

and declined with week of clutch initiation ($\chi^2 = 11.7$, $df = 1$, $P < 0.001$). The logistic regression equation for the probability of parasitism (p) in 2004 was $\text{logit}(p) = 2.73 + 1.88(\text{treatment}) - 0.49(\text{week})$. The odds of parasitism were 6.6 \times greater (95% CI: 1.8–23.9) at reference than at removal plots, and the odds of parasitism declined by 39% per week during the breeding season (odds ratio = 0.6, 95% CI: 0.4–0.8; Fig. 2A). In 2005, the probability of parasitism declined with week of clutch initiation ($\chi^2 = 15.1$, $df = 1$, $P < 0.001$),

but treatment was not significant ($\chi^2 = 0.59$, $df = 1$, $P = 0.42$). The equation for probability of parasitism in 2005 was: $\text{logit}(p) = 5.03 + 0.45(\text{treatment}) - 0.62(\text{week of first egg})$. The odds of parasitism were 1.6 \times (95% CI: 0.5–5.0) greater at reference than at removal plots and declined during the breeding season (odds ratio = 0.5, 95% CI: 0.4–0.8; Fig. 2B).

Multiple parasitism.—The number of cowbird eggs per parasitized Dickcissel nest was lowest at cowbird removal plots in 2004 (1.7 eggs per nest; range: 1–4) and highest at removal sites in 2005 (2.5; range: 1–6; Table 1). The number of cowbird eggs per parasitized nest did not covary with week of clutch initiation for any combination of year and treatment (linear regression, $F < 2.3$, $P > 0.14$). Overall, there was a significant interaction between year and treatment on the number of cowbird eggs per parasitized nest (linear analysis, $\chi^2 = 12.6$, $df = 5$, $P = 0.027$). In 2004, Dickcissel nests at cowbird removal plots averaged 0.6 fewer cowbird eggs per nest than nests at reference plots, but the difference was not significant ($\chi^2 = 6.6$, $df = 3$, $P = 0.086$). In 2005, Dickcissel nests in both treatments averaged 2.1 to 2.5 cowbird eggs per nest ($\chi^2 = 4.3$, $df = 5$, $P = 0.51$).

Clutch size of Dickcissels.—The average clutch size of Dickcissels varied with year and treatment (Table 1). In 2004, mean clutch size was 3.4 eggs per nest (range: 1–5) at cowbird removal plots and 3.3 (1–5) at reference plots. Mean clutch size was smaller in 2005, and averaged 2.3 eggs per nest (0–4) at cowbird removal plots and 2.4 (1–5) at reference plots. Clutch size did not covary with week of clutch initiation for any combination of year and treatment ($F < 1.2$, $P > 0.28$). Year and treatment had no interactive effect on clutch size of Dickcissels ($\chi^2 = 5.5$, $df = 5$, $P = 0.36$). In a main-effects model, clutch size of Dickcissels averaged 0.9–1.1 fewer eggs in 2005 than in 2004 ($\chi^2 = 21.5$, $df = 5$, $P < 0.001$) but did not differ between the two treatments ($\chi^2 = 1.2$, $df = 5$, $P = 0.94$).

Lag effects.—To test for lag effects after cessation of cowbird trapping, we compared demographic parameters for Dickcissel nests at two plots (20B, 20C) used for cowbird removals in 2004 and then as reference plots in 2005. Benefits of trapping were transitory. Percentage of nests parasitized increased from 51% to 82% ($\chi^2 = 10.1$, $df = 1$, $P = 0.002$), and the odds of parasitism were 4.3 \times (95% CI: 1.7–11.1) greater after cowbird trapping was discontinued. Number of cowbird eggs received increased from 1.7 to 2.1 eggs per parasitized nest ($\chi^2 = 5.1$, $df = 4$, $P = 0.28$), and clutch size of Dickcissels was reduced from 3.4 to 2.3 eggs per nest ($\chi^2 = 14.0$, $df = 4$, $P = 0.007$).

Nest survival.—Apparent nest survival was low in both years of our study: 34% ($n = 73$ nests of known fate) and 7% ($n = 84$) of nests were successful in 2004 and 2005, respectively. Most nest

TABLE 1. Percentage of Dickcissel nests parasitized by Brown-headed Cowbirds, number of cowbird eggs per parasitized nest, and number of Dickcissel eggs per nest (mean \pm SE) at treatment plots with cowbird removals and unmanipulated reference plots at Konza Prairie Biological Station, Kansas, 2004–2005. Numbers in parentheses are sample sizes of nests (n).

Year	Treatment	Percentage of nests parasitized	Number of cowbird eggs per parasitized nest	Number of Dickcissel eggs per nest
2004	Removal	51 (53)	1.7 \pm 0.2 (20)	3.4 \pm 0.2 (43)
	Reference	85 (27)	2.3 \pm 0.2 (20)	3.3 \pm 0.2 (24)
2005	Removal	78 (45)	2.5 \pm 0.2 (32)	2.3 \pm 0.2 (42)
	Reference	82 (44)	2.1 \pm 0.2 (33)	2.4 \pm 0.2 (41)

TABLE 2. Model fitting summary for the daily survival rate (S_d) of Dickcissel nests at cowbird removal and reference plots at Konza Prairie Biological Station, Kansas, 2004–2005. Model statistics include the deviance (Dev), number of parameters (K), Akaike's information criterion corrected for small sample sizes (AIC_c), difference from the minimum AIC_c model (ΔAIC_c), and Akaike weights (w_i). Model factors include experimental treatment (trt: cowbird removal or reference), year of study (year: 2004 or 2005), and day of season as an unconstrained time (time) or a linear (lin) seasonal trend. Factors were tested in factorial (\times) and main-effects models (+). We list candidate models that received support ($\Delta AIC_c < 5$ and $w_i \geq 0.03$) and selected starting models with the effects of treatment.

Model for S_d	Dev	K	AIC_c	ΔAIC_c	$w_i \leq$
year + lin	477.9	3	483.9	0.0	0.440
year \times lin	479.6	4	484.6	0.7	0.310
year	483.0	2	487.0	3.1	0.093
trt + lin	477.5	5	487.5	3.6	0.074
trt + year	482.8	3	488.8	4.8	0.039
trt \times year	482.7	4	490.7	6.8	0.015
trt	492.3	2	496.3	12.4	0.001
trt \times time	363.1	240	984.8	500.9	0.001

failures were caused by complete loss of eggs or young (2004: 77%, $n = 48$ failed nests; 2005: 90%, $n = 79$). In one instance, a Yellow-bellied Racer (*Coluber constrictor*) was observed eating a clutch of eggs. Less than a quarter of nest failures were attributable to abandonment of eggs in the nest after puncture of host egg(s) or partial clutch loss (2004: 21%, 2005: 8%). Nest abandonment was not caused by addition of parasitic eggs alone. Moreover, apparent nest survival was not related to nest parasitism status in either 2004 (parasitized: 40% successful, $n = 48$ nests; unparasitized: 24%, $n = 25$; Fisher's exact test: $P = 0.21$) or 2005 (parasitized: 9% successful, $n = 70$; unparasitized: 0%, $n = 15$; Fisher's exact test: $P = 0.58$). The remaining losses were attributable to flooding of nests by heavy rainfall and mortality of young from heat stress (3.1%).

The minimum AIC_c model for S_d of Dickcissel nests was a main-effects model with year and a linear seasonal trend in S_d over the breeding season (Table 2). The two next best models included a factorial model with year and a linear seasonal trend and a model with year alone. Together, these three models received $>7\times$ the support of all candidate models that included experimental treatment (trt) as a factor. The equation for probability of nest survival (p) from the minimum AIC_c model was $\text{logit}(p) = 2.55 + 0.57(\text{year}) - 0.19(\text{linear})$. Thus, odds of a nest surviving were $1.8\times$ (95% CI: 1.2–2.6) greater in 2004 than in 2005, and odds of nest survival declined by 17% per day during the breeding season (odds ratio = 0.83, 95% CI: 0.70–0.98; Fig. 3). Overall estimates of daily survival for Dickcissel nests (from model S_d trt \times year) were 0.924 ± 0.013 (SE; nest survival = 15%) and 0.922 ± 0.018 (nest survival = 14%) for nests in removal and reference plots in 2004, and 0.875 ± 0.019 (nest survival = 4%) and 0.858 ± 0.021 (nest survival = 3%) for nests in removal and reference plots in 2005.

Fledging rates.—We calculated fledging rates for successful nests that survived both the incubation and brood-rearing periods. Few nests survived the 24 days until fledging, and we pooled across treatments and years to estimate the number of fledglings produced per egg. Fledging rates were higher among parasitic cowbirds (0.81 ± 0.08 fledglings per parasitic egg; $n = 16$ nests) than among their Dickcissel hosts (0.61 ± 0.06 fledglings per host egg, $n = 21$), but the difference was marginally nonsignificant ($t_{35} = 2.0$, $P = 0.053$).

Estimates of productivity per nest.—The estimated nest productivity of Dickcissels did not differ between nests at cowbird removal plots ($\hat{P}_n = 0.32 \pm 0.16$ host fledglings per nest, 95% CI: 0.09–0.73) and at reference plots in 2004 ($\hat{P}_n = 0.29 \pm 0.18$; 95% CI: 0.07–0.79; bootstrap test, $P = 0.49$) or between nests at removal ($\hat{P}_n = 0.06 \pm 0.05$; 95% CI: 0–0.21) and reference plots in 2005 ($\hat{P}_n = 0.04 \pm 0.04$; 95% CI: 0.01–0.16; $P = 0.48$). Productivity of Dickcissels was significantly lower in the second year of our study because our mean estimates of productivity per nest for 2005 were not enclosed within the 95% CI for the 2004 estimates, and vice versa. We found similar patterns in the nest productivity of cowbirds. In 2004, the estimated productivity of cowbirds was lowered by $\sim 50\%$ at removal plots ($\hat{P}_n = 0.10 \pm 0.16$ cowbird fledglings per Dickcissel nest, 95% CI: 0–0.75) compared to reference plots ($\hat{P}_n = 0.22 \pm 0.21$;

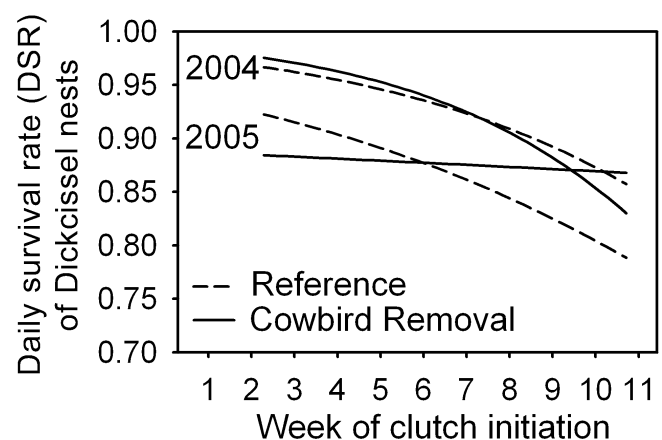


FIG. 3. Seasonal variation in daily survival rates (S_d) for Dickcissel nests at reference plots (2004, $n = 25$; 2005, $n = 42$) and cowbird removal plots (2004, $n = 48$; 2005, $n = 41$) at Konza Prairie Biological Station, Kansas. Estimates of S_d were calculated with the nest-survival procedure in MARK and taken from model year \times linear (Table 2). Seasonal variation in S_d was linear on a logit scale and curvilinear after back-transformation. Confidence intervals are omitted for clarity. Week 1 = 16–22 May.

95% CI: 0–0.80), but the difference was nonsignificant ($P=0.13$). In 2005, productivity of cowbirds was limited by nest predation, and similar numbers of parasitic young were produced from nests at removal ($\hat{P}_n = 0.07 \pm 0.08$; 95% CI: 0–0.32) and at reference plots ($\hat{P}_n = 0.04 \pm 0.04$; 95% CI: 0–0.21; $P=0.44$).

Estimates of population growth.—Our highest rate of nest productivity (\hat{P}_n) was 0.32 Dickcissel fledglings per nest at removal plots in 2004. We lack data on reneesting and survival rates because females were not individually marked. Elsewhere, Dickcissels reneest after clutch loss and average 1.2 nests per female per season (A ; Walk et al. 2004, Fletcher et al. 2006). If the sex ratio at fledging is even, maximum seasonal fecundity ($\hat{F}_s = \hat{A}\hat{P}_n/2$) for our study population may be 0.19 female fledglings per breeding female Dickcissel. Adult survival rates of female Dickcissels (\hat{S}_a) are unknown, but males have return rates of 10–49% (Zimmerman and Finck 1989, Fletcher et al. 2006), and juvenile survival rates (\hat{S}_j) may be as high as 50% of adult survival (McCoy et al. 1999, Fletcher et al. 2006). Overall, our most optimistic estimate of the finite rate of population change ($\lambda = F_s S_j + S_a$) for Dickcissels at Konza Prairie would be $\lambda = 0.54$ if $\hat{S}_a = 0.49$, and our highest estimate of nest productivity would require annual survival rates $\hat{S}_a \geq 0.91$ to realize a stationary rate of population change ($\lambda = 1$).

DISCUSSION

Our field study is the first attempt to examine the effects of cowbird removals on the productivity of a grassland songbird, and our major results were threefold. First, Dickcissels were heavily parasitized as a songbird host at our field site in northeast Kansas. A high proportion of nests received cowbird eggs, and multiple parasitism was common. Second, we reduced the effects of cowbirds because the odds of parasitism were 1.6–6.6 times greater at reference than at removal plots, but the effect was statistically significant in only one of two years. Last, the probability of nest predation did not differ between removal and reference plots. Dickcissels could have benefited from reductions in parasitism in 2004, but high rates of nest predation led to low rates of nest productivity for host and parasitic young in both years of our study.

Parasitism and predation.—Cowbirds were abundant on our study plots at Konza Prairie in 2004–2005 (Powell 2006), and tall-grass prairie sites in northeast Kansas contain some of the highest densities of cowbirds in the Flint Hills region (Jensen and Cully 2005a, b). Our sample of trapped cowbirds was predominantly male, which may reflect a male-biased sex ratio among adult cowbirds (Yokel 1989, Woolfenden et al. 2001) or a greater susceptibility to trapping among males (Rothstein et al. 1987).

Our estimates of the frequency of brood parasitism (>81%) and multiple parasitism (>2.1 cowbird eggs per nest) at reference plots were comparable to previous estimates for Dickcissels breeding in northeast Kansas: >79% and >2.5 (Jensen and Cully 2005b), >84% and >2.0 (Zimmerman 1983), and up to 95% and 2.4 (Elliott 1978). Source–sink dynamics may be an important part of the regional population dynamics of Dickcissels, because the frequency and magnitude of cowbird parasitism are much lower in southern Kansas, Oklahoma, and Missouri: 0–20% and 0–1.2

(Jensen and Cully 2005b), 9% and 1.4 (Winter 1999), and 19% (Patten et al. 2006). Similarly, our estimates of nest survival (3–15%) were comparable to Mayfield estimates of nest survival for Dickcissels in Kansas and Iowa (14%; Patterson and Best 1996, Hughes et al. 1999) but were lower than estimates from Oklahoma and Missouri (12–45%, McCoy et al. 1999; 19%, Rohrbaugh et al. 1999; and 30%, Winter 1999). The combined effects of parasitism and predation in the present study led to estimates of nest productivity for Dickcissels (0.04–0.32 fledglings per nest) that were considerably lower than productivity rates reported by previous studies (0.72–0.87, Zimmerman 1982; 0.77–1.06, Walk et al. 2004; 1.70, Winter 1999). Finally, a simple population model combining our highest rates of nest productivity with published estimates of demographic parameters indicated that Dickcissel populations at Konza Prairie were unlikely to be viable without multiple brooding, immigration, or higher rates of survival.

Despite removal of substantial numbers of cowbirds, high rates of nest predation reduced the potential benefits of reductions in parasitism for Dickcissels at Konza Prairie. Brood parasitism and nest predation have interactive effects in some songbird hosts (Arcese et al. 1996, Zanette et al. 2007), but we found little evidence that cowbirds were a major source of nest loss for Dickcissels. Few Dickcissel nests were abandoned because of cowbird activity, and nest survival was not affected by parasitism status. Moreover, parasitism and nest survival were not negatively correlated, as would be predicted by cowbird activity; instead, both rates declined simultaneously over the breeding season. The nest predator was determined for only one nest in our study: a clutch depredated by a Yellow-bellied Racer. Snakes are documented predators of songbirds at Konza Prairie; stomach contents have contained Dickcissel eggs and nestlings (Cavitt 1999, 2000). We were unable to determine the relative importance of different species of predators, but predator guilds are often diverse in grassland ecosystems, including snakes, small rodents, mid-sized carnivores, and deer (Thompson et al. 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003, Peer 2006).

Effects of cowbird removals on songbird hosts.—With intensive trapping effort in a region of high cowbird abundance, we successfully reduced brood parasitism of Dickcissels from 85% to 51%, and multiple parasitism from 2.3 to 1.7 cowbird eggs per parasitized nest, in the first year of the study. Despite a two-fold increase in the number of cowbirds trapped, cowbird removals had no significant effect on parasitism rates in the second year of the study. Overall, nest productivity did not differ between treatments in either year. By contrast, vireos nesting in the same study plots benefited from cowbird removals in both years. The percentage of vireo nests parasitized was reduced from 77–85% at reference plots to 47–58% at cowbird plots, which doubled the nest productivity of vireos from 0.4 to 1.1 fledglings per nest (Kosciuch and Sandercock 2008). Elsewhere, two additional studies have compared songbird productivity between cowbird removal and reference plots. Cowbird removals had little effect on nest productivity of Hooded Warblers (*Wilsonia citrina*; Stutchbury 1997) but doubled productivity of Song Sparrows (*Melospiza melodia*) from 0.5 to >1.0 fledglings per nest at reference and removal plots, respectively (Smith et al. 2002).

The present study demonstrates that the efficacy of cowbird removal programs must be evaluated empirically, because effects

may vary among species of hosts, including syntopic species of songbirds breeding in the same habitat. Dickcissels may have received less benefit from cowbird removals than vireos for three reasons. First, Dickcissels may be preferentially parasitized because this species arrives later in the breeding season and is still actively nesting in June, because their grassland nests are more easily located by cowbirds, or because cowbird young have higher survival in Dickcissel nests (0.81 fledglings per parasitic egg; present study) than in vireo nests (0.15 fledglings per parasitic egg; Kosciuch and Sandercock 2008). Second, Dickcissels can raise mixed broods of parasitic and host young (Zimmerman 1983, Peer 2006, present study), whereas vireos suffer complete reproductive failure if a cowbird egg is accepted (Parker 1999, Kosciuch and Sandercock 2008). Finally, songbirds may differ in their behavioral responses to removal of host eggs by cowbirds. The proximate cues for nest desertion by Dickcissels are poorly known (Peer et al. 2000). In vireos, nest desertion is driven by removal of host eggs and not by addition of cowbird eggs (Kus 1999, Kosciuch et al. 2006). Understanding the behavioral ecology of host–parasite interactions is critical to predicting the demographic effects of cowbird removals. Our cowbird removals unexpectedly increased the productivity of cowbirds from vireo nests by reducing nest desertion rates, an outcome that would be undesirable in management of threatened songbirds (Kosciuch and Sandercock 2008).

Improving the efficacy of cowbird removals.—We deployed cowbird traps at high densities (1 trap per 11 ha) and removed large numbers of cowbirds per year (>300), yet we concluded that cowbird removals may have limited utility for management of Dickcissels. The benefits of cowbird trapping were transient, because parasitism rates for Dickcissels and vireos at removal plots returned to background levels within one year after trapping was discontinued (Kosciuch and Sandercock 2008, present study). High rates of parasitism could have been caused by immigration of cowbirds from surrounding areas or by density-dependent changes in egg production among female cowbirds that eluded our traps (Rothstein et al. 1987, Jensen and Cully 2005a).

Cowbird removal programs reduce survival rates of juvenile and adult cowbirds. Our trapping of female cowbirds could have been more effective if we had deployed traps closer to preferred foraging sites, used playback of vocalizations to increase conspecific attraction (Dufty 1982, Rothstein et al. 1987), or combined cowbird trapping with shooting of females (Kostecke et al. 2003, 2005). On the other hand, population models suggest that egg survival may have the greatest influence on the rate of population change for cowbirds (Citta and Mills 1999). Removal or adding of cowbird eggs and nestlings could benefit Dickcissels through improvements in nest productivity (Whitfield et al. 1999; Kus 1999, 2002; Morrison and Averill-Murray 2002). Still, manipulation of cowbird eggs may be an impractical strategy because searching for songbird nests is labor-intensive.

Development of improved methods for removal of parasitic cowbirds or their young may have little benefit for Dickcissels, given that predation limited nest productivity, especially in the second year of our study. Predation also has greater effects on productivity than parasitism in other managed populations of songbirds (Braden et al. 1997, Stutchbury 1997, Morrison and Averill-Murray 2002). To date, few studies have tested the effects of predator removals on songbird productivity. Removal of carnivores

(Raccoon [*Procyon lotor*], Striped Skunk [*Mephitis mephitis*], and Red Fox [*Vulpes vulpes*]) did not improve nest survival of grassland birds, because of a numerical response in ground squirrels (*Spermophilus* spp.; Dion et al. 1999). However, removals of corvids (Magpie [*Pica pica*] and Carrion Crow [*Corvus corone*]), small mammals (White-footed Mouse [*Peromyscus leucopus*] and Eastern Chipmunk [*Tamias striatus*]), and mammalian predators (mustelids, Hedgehogs [*Erinaceus europaeus*], and Red Fox) increased nest survival for farmland songbirds (Stoate and Szczer 2001), Veery (*Catharus fuscescens*; Schmidt et al. 2001), and Sky Larks (*Alauda arvensis*; Donald et al. 2002), respectively. At our study site, predator removals may increase productivity of host species of songbirds but could also benefit cowbirds, because parasitism rates were high. To date, no field study has examined songbird fecundity in response to a factorial manipulation of brood parasitism and nest predation. Cowbird removal programs would be aided by a better understanding of the interactive effects of parasitism and predation on songbird productivity.

Alternatives to removals of cowbirds and predators.—Programs that remove cowbirds or native predators for conservation purposes are often labor-intensive, result in few long-term benefits, and have ethical considerations (Côté and Sutherland 1997, Rothstein and Peer 2005). For Dickcissels in the Flint Hills region of eastern Kansas, the best alternatives to cowbird removal programs may be changes in habitat management. First, protection of large grassland tracts is desirable, because rates of brood parasitism and nest predation tend to be lower in large prairie fragments (Winter and Faaborg 1999, Davis and Sealy 2000, Herkert et al. 2003). Second, nest productivity often decreases with proximity to shrub and forest edges (Winter et al. 2000, 2005; Jensen and Finck 2004; Renfrew et al. 2005; Patten et al. 2006), possibly because woody plants provide perch sites for nest-searching cowbirds (Hauber and Russo 2000, Jensen and Cully 2005a) or cover for nest predators (Blouin-Demers and Weatherhead 2001, Renfrew and Ribic 2003, Renfrew et al. 2005). Prescribed fire can control spread of woody plants and reduce cowbird parasitism (Best 1979, Clotfelter et al. 1999, Briggs et al. 2002), though nest predation may be higher immediately after a burn (Cavitt 1999, Rohrbaugh et al. 1999, Shochat et al. 2005). Finally, intensive grazing can have negative effects if livestock trample nests, remove nest cover, or provide foraging sites for cowbirds (Morris and Thompson 1998, Rohrbaugh et al. 1999). Reductions in cattle densities could benefit songbird hosts by reducing cowbird activity, by providing greater nest cover, or by increasing mortality of woody plants with hotter fires (Winter 1999, Goguen and Mathews 2001, Kostecke et al. 2003, Winter et al. 2005). In the future, field tests of rangeland practices that reduce parasitism and predation may help to identify the best management strategies for grassland songbirds of conservation concern.

ACKNOWLEDGMENTS

We thank J. Bowers, T. Conkling, J. Larkins, R. Lohnes, J. K. Nooker, T. H. Parker, J. W. Rivers, and T. Van Slyke for logistical support in the field. H. Greene, W. Hochachka, I. J. Lovette, D. W. Winkler, and the Cornell University Honors Program provided assistance and feedback with preliminary data analyses. W. E. Jensen, P. E. Klug, J. K. Nooker, and several anonymous reviewers

made constructive comments on drafts of our manuscript. Field work for this project was supported by grants from the National Science Foundation, including a Research Experiences for Undergraduates Site grant (DBI-0243890) and the Konza Prairie Long-term Ecological Research program (DEB-0218210), by a University Small Research Grant (USRG) from Kansas State University (K-State), and by a research grant from the Kansas Ornithological Society. B.K.S. and K.L.K. were supported by the Division of Biology at K-State. Research activities were conducted under permits from federal (U.S. Fish and Wildlife Service) and state wildlife agencies (Kansas Department of Wildlife and Parks), and field protocols were approved by the Institutional Animal Care and Use Committee at K-State.

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.
- BASILL, G. D., AND S. A. TEMPLE. 1999. Winter ecology, behavior, and conservation needs of Dickcissels in Venezuela. Pages 289–299 *in Ecology and Conservation of Grassland Birds of the Western Hemisphere* (P. D. Vickery and J. R. Herkert, Eds.). *Studies in Avian Biology*, no. 19.
- BERKELEY, L. I., J. P. MCCARTY, AND L. L. WOLFENBARGER. 2007. Postfledging survival and movement in Dickcissels (*Spiza americana*): Implications for habitat management and conservation. *Auk* 124:396–409.
- BEST, L. B. 1979. Effects of fire on a Field Sparrow population. *American Midland Naturalist* 101:434–442.
- BLOUIN-DEMERS, G., AND P. J. WEATHERHEAD. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82:2882–2896.
- 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.
- BRENNAN, L. A., AND W. P. KUVLESKY, JR. 2005. North American grassland birds: An unfolding conservation crisis? *Journal of Wildlife Management* 69:1–13.
- 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.
- CAVITT, J. F. 1999. Effects of prairie fire and grazing on Brown Thrasher nest predation. *Proceedings of the North American Prairie Conference* 16:112–119.
- CAVITT, J. F. 2000. Tallgrass prairie snake assemblage: Food habits. *Herpetological Review* 31:47–48.
- CITTA, J. J., AND L. S. MILLS. 1999. What do demographic sensitivity analyses tell us about controlling Brown-headed Cowbirds? Pages 121–134 *in Research and Management of the Brown-headed Cowbird in Western Landscapes* (M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, Eds.). *Studies in Avian Biology*, no. 18.
- CLOTFELTER, E. D., K. YASUKAWA, AND R. D. NEWSOME. 1999. The effects of prescribed burning and habitat edges on Brown-headed Cowbird parasitism of Red-winged Blackbirds. Pages 275–281 *in Research and Management of the Brown-headed Cowbird in Western Landscapes* (M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, Eds.). *Studies in Avian Biology*, no. 18.
- CÔTÉ, I. M., AND W. J. SUTHERLAND. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11:395–405.
- DAVIS, S. K., AND S. G. SEALY. 2000. Cowbird parasitism and nest predation in fragmented grasslands of southwestern Manitoba. Pages 220–228 *in Ecology and Management of Cowbirds and Their Hosts* (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.
- 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, 1972–1995. Pages 333–341 *in Ecology and Management of Cowbirds and Their Hosts* (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- DION, N., K. A. HOBSON, AND S. LARIVIÈRE. 1999. Effects of removing duck-nest predators on nesting success of grassland songbirds. *Canadian Journal of Zoology* 77:1801–1806.
- DONALD, P. F., A. D. EVANS, L. B. MUIRHEAD, D. L. BUCKINGHAM, W. B. KIRBY, AND S. I. A. SCHMITT. 2002. Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis* 144:652–664.
- DUFTY, A. M., JR. 1982. Response of Brown-headed Cowbirds to simulated conspecific intruders. *Animal Behaviour* 30:1043–1052.
- ELLIOTT, P. F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. *Auk* 95:161–167.
- 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.
- GOGUEN, C. B., AND N. E. MATHEWS. 2001. Brown-headed Cowbird behavior and movements in relation to livestock grazing. *Ecological Applications* 11:1533–1544.
- GOTELLI, N. J., AND A. M. ELLISON. 2004. *A Primer of Ecological Statistics*. Sinauer Associates, Sutherland, Massachusetts.
- 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* 118:765–769.
- GROSS, A. O. 1921. The Dickcissel (*Spiza americana*) of the Illinois prairies. *Auk* 38:163–184.
- HAUBER, M. E., AND S. A. RUSSO. 2000. Perch proximity correlates with higher rates of cowbird parasitism of ground nesting Song Sparrows. *Wilson Bulletin* 112:150–153.
- HERKERT, J. R., D. L. REINKING, D. A. WIEDENFELD, M. WINTER, J. L. ZIMMERMAN, W. E. JENSEN, E. J. FINCK, R. R. KOFORD, D. H. WOLFE, S. K. SHERROD, AND OTHERS. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the mid-continental United States. *Conservation Biology* 17:587–594.
- HOOVER, J. P. 2003. Multiple effects of brood parasitism reduce the reproductive success of Prothonotary Warblers, *Protonotaria citrea*. *Animal Behaviour* 65:923–934.

- HUGHES, J. P., R. J. ROBEL, K. E. KEMP, AND J. L. ZIMMERMAN. 1999. Effects of habitat on Dickcissel abundance and nest success in conservation reserve program fields in Kansas. *Journal of Wildlife Management* 63:523–529.
- JENSEN, W. E., AND J. F. CULLY, JR. 2005a. Density-dependent habitat selection by Brown-headed Cowbirds (*Molothrus ater*) in tallgrass prairie. *Oecologia* 142:136–149.
- JENSEN, W. E., AND J. F. CULLY, JR. 2005b. Geographic variation in Brown-headed Cowbird (*Molothrus ater*) parasitism on Dickcissels (*Spiza americana*) in Great Plains tallgrass prairie. *Auk* 122:648–660.
- JENSEN, W. E., AND E. J. FINCK. 2004. Edge effects on nesting Dickcissels (*Spiza americana*) in relation to edge type of remnant tallgrass prairie in Kansas. *American Midland Naturalist* 151:192–199.
- KOSCIUCH, K. L., T. H. PARKER, AND B. K. SANDERCOCK. 2006. Nest desertion by a cowbird host: An antiparasite behavior or a response to egg loss? *Behavioral Ecology* 17:917–924.
- KOSCIUCH, K. L., AND B. K. SANDERCOCK. 2008. Cowbird removals unexpectedly increase productivity of a brood parasite and the songbird host. *Ecological Applications* 18:537–548.
- KOSTECKE, R. M., J. A. KOLOSZAR, AND D. C. DEARBORN. 2003. Effect of a reduction in cattle stocking rate on Brown-headed Cowbird activity. *Wildlife Society Bulletin* 31:1083–1091.
- KOSTECKE, R. M., S. G. SUMMERS, G. H. ECKRICH, AND D. A. CIMPRICH. 2005. Effects 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 *Management of Cowbirds and Their Hosts: Balancing Science, Ethics, and Mandates* (C. P. Ortega, J. F. Chace, and B. D. Peer, Eds.). *Ornithological Monographs*, no. 57.
- KUS, B. E. 1999. Impacts of Brown-headed Cowbird parasitism on productivity of the endangered Least Bell's Vireo. Pages 160–166 in *Research and Management of the Brown-headed Cowbird in Western Landscapes* (M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, Eds.). *Studies in Avian Biology*, no. 18.
- 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 Vireos (*Vireo bellii pusillus*) and Southwestern Willow Flycatchers (*Empidonax traillii extimus*) to cowbird (*Molothrus* spp.) control. Pages 16–27 in *Management of Cowbirds and Their Hosts: Balancing Science, Ethics, and Mandates* (C. P. Ortega, J. F. Chace, and B. D. Peer, Eds.). *Ornithological Monographs*, no. 57.
- 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 of London, Series B* 265:249–254.
- LLOYD, J. D., AND T. E. MARTIN. 2005. Reproductive success of Chestnut-collared Longspurs in native and exotic grassland. *Condor* 107:363–374.
- LONG, C. A., C. F. LONG, J. KNOPS, AND D. H. MATULIONIS. 1965. Reproduction in the Dickcissel. *Wilson Bulletin* 77:251–256.
- MCCOY, T. D., M. R. RYAN, E. W. KURZEJESKI, AND L. W. BURGER, JR. 1999. Conservation reserve program: Source or sink habitat for grassland birds in Missouri? *Journal of Wildlife Management* 63:530–538.
- 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.
- MCLAREN, C. M., B. E. WOOLFENDEN, H. L. GIBBS, AND S. G. SEALY. 2003. Genetic and temporal patterns of multiple parasitism by Brown-headed Cowbirds (*Molothrus ater*) on Song Sparrows (*Melospiza melodia*). *Canadian Journal of Zoology* 81:281–286.
- MORRIS, D. L., AND F. R. THOMPSON III. 1998. Effects of habitat and invertebrate density on abundance and foraging behavior of Brown-headed Cowbirds. *Auk* 115:376–385.
- MORRISON, M. L., AND A. AVERILL-MURRAY. 2002. Evaluating the efficacy of manipulating cowbird parasitism on host nesting success. *Southwestern Naturalist* 47:236–243.
- MURPHY, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. *Auk* 120:20–34.
- ORTEGA, C. P., AND J. C. ORTEGA. 2001. Effects of Brown-headed Cowbirds on the nesting success of Chipping Sparrows in southwest Colorado. *Condor* 103:127–133.
- PARKER, T. H. 1999. Responses of Bell's Vireos to brood parasitism by the Brown-headed Cowbird in Kansas. *Wilson Bulletin* 111:499–504.
- PATTEN, M. A., E. SHOCHAT, D. L. REINKING, D. H. WOLFE, AND S. K. SHERROD. 2006. Habitat edge, land management, and rates of brood parasitism in tallgrass prairie. *Ecological Applications* 16:687–695.
- PATTERSON, M. P., AND L. B. BEST. 1996. Bird abundance and nesting success in Iowa CRP fields: The importance of vegetation structure and composition. *American Midland Naturalist* 135:153–167.
- PEER, B. D. 2006. Egg destruction and egg removal by avian brood parasites: Adaptiveness and consequences. *Auk* 123:16–22.
- PEER, B. D., S. K. ROBINSON, AND J. R. HERKERT. 2000. Egg rejection by cowbird hosts in grasslands. *Auk* 117:892–901.
- PIETZ, P. J., AND D. A. GRANFORS. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64:71–87.
- POWELL, A. F. L. A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. *Auk* 123:183–197.
- RENFREW, R. B., AND C. A. RIBIC. 2003. Grassland passerine nest predators near pasture edges identified on videotape. *Auk* 120:371–383.
- RENFREW, R. B., C. A. RIBIC, AND J. L. NACK. 2005. Edge avoidance by nesting grassland birds: A futile strategy in a fragmented landscape. *Auk* 122:618–636.
- RICH, T. D., C. J. BEARDMORE, H. BERLANGA, P. J. BLANCHER, S. W. BRADSTREET, G. S. BUTCHER, D. W. DEMAREST, E. H. DUNN, W. C. HUNTER, E. E. IÑIGO-ELIAS, AND OTHERS. 2004. *Partners in Flight North American Landbird Conservation Plan*. Cornell Lab of Ornithology, Ithaca, New York.
- ROBBINS, M. B., A. T. PETERSON, AND M. A. ORTEGA-HUERTA. 2002. Major negative impacts of early intensive cattle stocking on tallgrass prairies: The case of the Greater Prairie Chicken (*Tympanuchus cupido*). *North American Birds* 56:239–244.
- ROBINSON, S. K., F. R. THOMPSON III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.

- ROGERS, C. M., M. J. TAITT, J. N. M. SMITH, AND G. JONGEJAN. 1997. Nest predation and cowbird parasitism create a demographic sink in wetland-breeding Song Sparrows. *Condor* 99:622–633.
- ROHRBAUGH, R. W., JR., D. L. REINKING, D. H. WOLFE, S. K. SHERROD, AND M. A. JENKINS. 1999. Effects of prescribed burning and grazing on nesting and reproductive success of three grassland passerine species in tallgrass prairie. Pages 165–170 in *Ecology and Conservation of Grassland Birds of the Western Hemisphere* (P. D. Vickery and J. R. Herkert, Eds.). *Studies in Avian Biology*, no. 19.
- 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 *Management of Cowbirds and Their Hosts: Balancing Science, Ethics, and Mandates* (C. P. Ortega, J. F. Chace, and B. D. Peer, Eds.). *Ornithological Monographs*, no. 57.
- ROTHSTEIN, S. I., J. VERNER, E. STEVENS, AND L. V. RITTER. 1987. Behavioral differences among sex and age classes of the Brown-headed Cowbird and their relation to the efficacy of a control program. *Wilson Bulletin* 99:322–337.
- SCHMIDT, K. A., J. R. GOHEEN, R. NAUMANN, R. S. OSTFELD, E. M. SCHAUBER, AND A. BERKOWITZ. 2001. Experimental removal of strong and weak predators: Mice and chipmunks preying on songbird nests. *Ecology* 82:2927–2936.
- SCHMIDT, K. A., AND C. J. WHELAN. 1999. The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. *Conservation Biology* 13:46–57.
- SHOCHAT, E., M. A. PATTEN, D. W. MORRIS, D. L. REINKING, D. H. WOLFE, AND S. K. SHERROD. 2005. Ecological traps in isodars: Effects of tallgrass prairie management on bird nest success. *Oikos* 111:159–169.
- 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.
- STOATE, C., AND J. SZCZUR. 2001. Could game management have a role in the conservation of farmland passerines? A case study from a Leicestershire farm. *Bird Study* 48:279–292.
- STUTCHBURY, B. J. M. 1997. Effects of female cowbird removal on reproductive success of Hooded Warblers. *Wilson Bulletin* 109:74–81.
- SUEDKAMP WELLS, K. M., M. R. RYAN, J. J. MILLSPAUGH, F. R. THOMPSON III, AND M. W. HUBBARD. 2007. Survival of post-fledging grassland birds in Missouri. *Condor* 109:781–794.
- THOMPSON, F. R., III, W. DIJACK, AND D. E. BURHANS. 1999. Video identification of predators at songbird nests in old fields. *Auk* 116:259–264.
- WALK, J. W., K. WENTWORTH, E. L. KERSHNER, E. K. BOLLINGER, AND R. E. WARNER. 2004. Renesting decisions and annual fecundity of female Dickcissels (*Spiza americana*) in Illinois. *Auk* 121:1250–1261.
- WARD, D., AND J. N. M. SMITH. 2000. Brown-headed Cowbird parasitism results in a sink population in Warbling Vireos. *Auk* 117:337–344.
- WHITEHEAD, M. A., S. H. SCHWEITZER, AND W. POST. 2000. Impact of brood parasitism on nest survival parameters and seasonal fecundity of six songbird species in southeastern old-field habitat. *Condor* 102:946–950.
- WHITFIELD, M. J., K. M. ENOS, AND S. P. ROWE. 1999. Is Brown-headed Cowbird trapping effective for managing populations of the endangered Southwestern Willow Flycatcher? Pages 260–266 in *Research and Management of the Brown-headed Cowbird in Western Landscapes* (M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, Eds.). *Studies in Avian Biology*, no. 18.
- WINTER, M. 1999. Nesting biology of Dickcissels and Henslow's Sparrows in southwestern Missouri prairie fragments. *Wilson Bulletin* 111:515–526.
- WINTER, M., AND J. FAABORG. 1999. Patterns of area sensitivity in grassland-nesting birds. *Conservation Biology* 13:1424–1436.
- WINTER, M., D. H. JOHNSON, AND J. FAABORG. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. *Condor* 102:256–266.
- WINTER, M., D. H. JOHNSON, AND J. A. SHAFFER. 2005. Variability in vegetation effects on density and nesting success of grassland birds. *Journal of Wildlife Management* 69:185–197.
- WOODWORTH, B. L. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conservation Biology* 13:67–76.
- WOOLFENDEN, B. E., H. L. GIBBS, AND S. G. SEALY. 2001. Demography of Brown-headed Cowbirds at Delta Marsh, Manitoba. *Auk* 118:156–166.
- YOKEL, D. A. 1989. Intrasexual aggression and the mating behavior of Brown-headed Cowbirds: Their relation to population densities and sex ratios. *Condor* 91:43–51.
- ZANETTE, L., D. T. HAYDON, J. N. M. SMITH, M. J. TAITT, AND M. CLINCHY. 2007. Reassessing the cowbird threat. *Auk* 124:210–223.
- ZANETTE, L., E. MACDOUGALL-SHAKLETON, M. CLINCHY, AND J. N. M. SMITH. 2005. Brown-headed Cowbirds skew host offspring sex ratios. *Ecology* 86:815–820.
- ZIMMERMAN, J. L. 1982. Nesting success of Dickcissels (*Spiza americana*) in preferred and less preferred habitats. *Auk* 99:292–298.
- ZIMMERMAN, J. L. 1983. Cowbird parasitism of Dickcissels in different habitats and at different nest densities. *Wilson Bulletin* 95:7–22.
- ZIMMERMAN, J. L. 1984. Nest predation and its relationship to habitat and nest density in Dickcissels. *Condor* 86:68–72.
- ZIMMERMAN, J. L., AND E. J. FINCK. 1989. Philopatry and correlates of territorial fidelity in male Dickcissels. *North American Bird Bander* 14:83–85.

Associate Editor: S. G. Sealy