HOST-PARASITE INTERACTIONS ON AN EXPERIMENTAL LANDSCAPE

by

KARL L. KOSCIUCH

B. S., East Stroudsburg University, 1997
M. S., Texas A&M University, 2002

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPY

Division of Biology
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Abstract

The reproductive strategies of avian brood parasites and the behavioral responses of their hosts have served as a model of co-evolution in nature. Host adaptations to reduce the costs of parasitism are countered with novel parasite behaviors that increase the success of the parasite and thereby decrease host productivity. Not all host species possess anti-parasite defense behaviors, and parasitism by Brown-headed Cowbirds (*Molothrus ater*) may cause population declines in some species. Bell's Vireo (*Vireo bellii*) is a small-bodied cowbird host that fails to fledge young if successfully parasitized. Although vireos desert naturally parasitized nests, the cues that cause desertion have not been identified. Understanding how parasitism affects vireo productivity is important because cowbird removal is an integral component of the recovery efforts for the endangered Least Bell's Vireo (*V. b. pusillus*) in California. However, it is generally unknown how cowbird removal affects vireo productivity. To address these issues, I monitored the productivity of vireos nesting in Kansas at the Konza Prairie Biological Station, conducted a clutch manipulation experiment, and experimentally removed cowbirds. In addition, I used stable isotope analysis to determine if recently fledged cowbird young could be assigned to habitats or host species. I found that vireos did not desert nests due to the presence of a cowbird egg; rather egg removal by cowbirds caused desertion, which is a generalized response in many taxa of birds. Cowbird removals decreased parasitism of vireo nests by approximately 36% and led to a 2-fold increase in vireo productivity per pair. Cowbird productivity from vireo pairs increased because fewer parasitized nests were deserted and parasitized nests on removal plots had a higher

probability of success. No cowbird removal study has reported an increase in cowbird productivity in response to trapping. Cowbird nestlings from prairie plots and shrub plots differed in carbon and nitrogen isotope compositions, and 87% of locally produced juvenile cowbirds were classified with nestlings from shrub plots. Thus, the continued expansion of woody plants into tallgrass prairie may result in local increases in cowbird productivity.

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11 years at universities, a monkey can still outdo me. Bill and Jim's enthusiasm and interest in cowbird biology is inspiring. Numerous graduate students at K-State took time to discuss their research interests and educate me about tallgrass prairie including Duncan McKinley and Jesse Nippert.

I thank my family for all of their love and support.

CHAPTER 1 - INTRODUCTION

Brood parasitism, a type of kleptoparasitism, occurs when offspring of one species steal the parental care of another species. Only 1% of the approximately 10,000 species of birds exhibit this rare reproductive strategy where the female lays an egg in the nest of a host species and abandons incubation and brood rearing to the foster parents (Rothstein and Robinson 1998). Brood parasites can cause moderate to severe fitness losses and the cost varies among parasite and host species. Honeyguides (Family Indicatoridae) and Old World cuckoos (Family Cucuclidae) cause large losses in host productivity because the parasitic nestling kills host nest-mates by stabbing them with the bill, or evicting them from the nest (Friedmann 1955, Davies and Brooke 1988). Despite high individual costs for some species, honeyguides and cuckoos occur at low densities and it is unlikely that parasitism has population level consequences for host species. Although nestlings of the host-generalist Brown-headed Cowbird (*Molothrus ater*) do not kill nest-mates, cowbirds possess life history traits that make them successful parasites. Cowbird eggs often hatch in a shorter period than host eggs, which confers a competitive advantage to cowbird nestlings because they may be larger than host nest mates and be more competitive in acquiring more food (Lichtenstein and Sealy 1998, Kilner et al. 2004). Species-specific costs of parasitism may also be influenced by host life history traits: small-bodied species that have long incubation periods (>12 days) suffer the highest costs (Hauber 2003). In addition, female cowbirds may remove host eggs before or after parasitizing a nest or destroy nests unsuitable for parasitism to induce hosts to renest (Sealy 1992, Arcese et al. 1996). Unlike cuckoos, cowbirds occur at high densities and cowbird parasitism may have population level

consequences for host species (Ward and Smith 2000, Morrison and Hahn 2002, Smith et al. 2002).

The costs of parasitism have led to the evolution of anti-parasite behaviors in some host species (Rothstein 1990). Egg ejection is the most prevalent defense against parasitism by cuckoo hosts, and many ejecters remove non-mimetic egg from the nest >80% of the time they are experimentally parasitized (Davies and Brooke 1989). Egg discrimination is not as well developed in cowbird hosts; only 24 of 220 host species regularly eject non-mimetic cowbird eggs (Peer and Sealy 2004). Small-bodied hosts physically unable to remove cuckoo or cowbird eggs exhibit alternative behavioral responses to parasitism: burial of parasitic eggs by construction of a new nest on top of the parasitized nest, or desertion of parasitized nests (Peer et al. 2005). Nest desertion is more common in cowbird hosts than cuckoo hosts, and the prevalence of desertion may be due to gape-size limitations or host life history traits (Servedio and Hauber 2006). While ejection of undamaged non-mimetic eggs is a co-evolved response to parasitism, nest desertion occurs in multiple contexts. In addition, many cowbird hosts that desert naturally parasitized nests do not desert experimentally parasitized nests (Hill and Sealy 1994). Thus, without experimental evidence it is difficult to determine if desertion is an evolved response to cowbird parasitism, or a response to general stimuli such as egg predation by cowbirds.

Cowbird parasitism can cause large losses in productivity and lead to population declines in small-bodied host species. Populations recently exposed to parasitism are at greatest risk because they lack defense behaviors. Cowbird removal through trapping is an important component of management programs for the endangered Least Bell's Vireo (*Vireo bellii pusillus*), Black-capped Vireo (*Vireo atricapillus*), Southwestern Willow Flycatcher (*Empidonax*

traillii extimus), and Kirtland's Warbler (*Dendroica kirtlandii*). However, the effects of cowbird removal are difficult to evaluate because applied studies often lack baseline data, do not have unmanipulated reference sites, or additional management activities (e.g., reduced cattle density) makes evaluating the effects of removal challenging (Kus 1999). The use of cowbird removal to aid in the recovery of songbird species has been challenged because the programs are open-ended, may divert funds from conservation of habitat, and kill thousands of cowbirds annually (Rothstein and Peer 2005). Thus, cowbird removal experiments with unmanipulated reference plots are needed to determine how cowbird removal, and the discontinuation of trapping affects host productivity.

Bell's Vireo (*V. b. bellii*) is an excellent study species to investigate the effects of brood parasitism by cowbirds for several reasons. First, it is a cowbird host throughout its range and variability in nest desertion frequencies exists among populations (Parker 1999, Kus 2002). Second, it fails to fledge young when successfully parasitized, making acceptance of cowbird eggs maladaptive. Third, it can be locally common and the nests are easy to locate. Vireos lay a modal clutch of 4 eggs in unparasitized nests. Incubation begins on the day the third egg is laid and lasts from approximately 14 days. The young fledge the nest in approximately 11 days and stay with the parents for up to 30 days after fledging. Cowbirds parasitize vireo nests during the vireo egg laying stage and often remove a host egg before or after parasitizing a nest. Cowbird eggs hatch in 11 days and the cowbird young has a competitive advantage in the nest because it is larger and receives most of the food. Thus, most vireo young that hatch in the presence of a cowbird nestling starve to death and are removed by the parents.

The goals of this dissertation were to integrate behavioral ecology, population biology, and stable isotope analysis to understand host-parasite interactions in an experimental landscape.

Specifically, my research objectives were to determine 1) what cue(s) causes nest desertion in a small-bodied host, Bell's Vireo, 2) how cowbird parasitism may limit the productivity of Bell's Vireos, and 3) if the habitat from which juvenile cowbird were produced could be identified using stable isotope analysis. The results from my research are applicable to current issues in evolutionary ecology and endangered species conservation biology.

This dissertation is organized into three core chapters. In chapter two, I tested two sets of hypotheses to determine if 1) nest desertion is a response to the addition of cowbird eggs or is a generalized response to egg loss, and 2) if environmental variance explains variability in the response of breeding pairs to parasitism. In chapter three, I used a cowbird removal experiment with a switchback design to determine how cowbird removals affect host and parasite productivity. I hypothesized that parasitism limits vireo productivity and influences several aspects of vireo and cowbird demography. I predicted that cowbird removals would increase vireo productivity, decrease nest desertion, increase survival of parasitized nests, and decrease cowbird productivity. In chapter four, I used stable carbon and nitrogen isotope analysis to determine if juvenile cowbirds could be assigned to habitat type, and if changes in diet post-fledging could be detected. Chapter five is a summary of the major findings of the studies.

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CHAPTER 2 - NEST DESERTION BY A COWBIRD HOST: AN ANTI-PARASITE BEHAVIOR OR A RESPONSE TO EGG LOSS?

Karl L. Kosciuch, Timothy H. Parker, and Brett K. Sandercock

ABSTRACT

Natural selection can favor songbirds that desert nests containing eggs of the parasitic Brown-headed Cowbird (*Molothrus ater*). However, the high variability in desertion of parasitized nests within species is perplexing in light of the typically high costs of parasitism. Because nest desertion can also be a response to partial clutch predation, we first asked if Bell's Vireos (*Vireo bellii*) deserted nests in response to the presence of cowbird eggs (anti-parasite response hypothesis), or to egg removal by predators and female cowbirds (egg predation hypothesis). Second, we asked whether variation in nest desertion was due to intrinsic differences among individuals or to variation in nest contents. We monitored a large number of nests ($n = 494$) and performed a clutch manipulation experiment to test these hypotheses. The number of vireo eggs that remained in a nest was a strong predictor of desertion both within and among pairs. Neither the presence of a single cowbird egg, which leads to nest failure for this host, nor the number of cowbird eggs received in a vireo nest influenced nest desertion. Furthermore, vireos did not desert experimental nests when we immediately exchanged cowbird eggs for vireo eggs, but deserted if we removed vireo eggs and replaced them with cowbird eggs the following morning. Desertion of parasitized nests by Bell's Vireos can be almost entirely explained as a response to partial or complete clutch loss, and does not appear to have been altered by selection from brood parasitism.

INTRODUCTION

The reproductive strategies of avian brood parasites and the behavioral responses of their hosts have served as a model of co-evolution in nature (Davies and Brooke 1989, Rothstein 1990, Røskaft and Moksnes 1998). Host adaptations to avoid parasitism are countered with novel parasite behaviors that increase the success of the parasite and thereby decrease host productivity (Davies and Brooke 1988, Rothstein 2001). Hosts that accept the highly mimetic eggs of the common cuckoo (*Cuculus canorus*) fail to fledge their own young because the cuckoo nestling ejects the hosts' eggs (Davies and Brooke 1989). Although Brown-headed Cowbird (*Molothrus ater*) nestlings do not eject host eggs or chicks, cowbird chicks may have a competitive advantage relative to host young if they hatch sooner, are larger relative to host young, and beg more aggressively for food (e.g., Goguen and Mathews 1996, Lorenzana and Sealy 1999, Kilner et al. 2004). In addition, female cowbirds may remove a host egg before or after laying a parasitic egg (Sealy 1992, 1994), and the presence of cowbird eggs or chicks can reduce the hatching success of host eggs (Hauber 2003, Hoover 2003). Last, female cowbirds may destroy the contents of unparasitized nests during incubation to induce hosts to renest (Arcese et al. 1996).

In response to the selective pressures exerted by brood parasites, several avian host species have co-evolved anti-parasite behaviors to reduce fitness costs. Egg ejection is well documented in many hosts that have long co-evolutionary histories with cuckoos, and some species eject greater then 80% of non-mimetic eggs (Davies and Brooke 1998). Egg discrimination is not as well developed in cowbird hosts; only 24 of 220 host species regularly reject non-mimetic cowbird eggs by removing eggs that differ from their own (Rothstein 1982a, Peer and Sealy 2004, Rothstein and Peer 2005). Small-bodied hosts physically unable to remove cuckoo or cowbird eggs exhibit alternative behavioral responses to parasitism: burial of parasitic

eggs by construction of a new nest on top of the parasitized nest, or desertion of parasitized nests (Davies and Brooke 1989, Sealy 1995, Hosoi and Rothstein 2000). Nest desertion is more common in cowbird hosts than cuckoo hosts, and the prevalence of desertion may be due to gape-size limitations or host life history traits (Servedio and Hauber 2006). While egg ejection frequencies tend to be consistent across the breeding range of cowbird hosts, variability in nest desertion frequencies in response to cowbird parasitism exists both within and among host populations (Rothstein 1990, Briskie et al. 1992, Hosoi and Rothstein 2000). Moreover, behavioral plasticity exists within individual breeding pairs with some both accepting and rejecting parasitic eggs within a breeding season (Budnik et al. 2001, Kus 2002). Variation in desertion frequency is puzzling because small-bodied host species suffer the highest costs of brood parasitism (Sealy 1996, Lorenzana and Sealy 1999).

While ejection of undamaged parasitic eggs may be a co-evolved response to brood parasitism in cuckoo and cowbird hosts, nest desertion occurs in multiple contexts and may have evolved independently of brood parasitism (Rothstein 1975, 1990, Ackerman and Eadie 2003). Although many cowbird hosts desert naturally parasitized nests, only Cedar Waxwings (*Bombycilla cedrorum*) are known to desert nests experimentally parasitized with cowbird eggs (Rothstein 1975, 1976). Other cues, such as egg removal by female cowbirds or activity of cowbirds at the nest, may be needed to induce desertion (Strausberger and Burhans 2001). Thus, egg loss may cause desertion in host species that may or may not possess specific anti-parasite behaviors (Rothstein 1982b, Hill and Sealy 1994, Smith et al. 2003).

Desertion in response to partial clutch or brood reduction is a behavior found in insects (Zink 2003), fish (Coleman et al. 1985, Jennions and Polakow 2001), and birds (Beissinger 1990, Ackerman et al. 2003). Parental investment theory predicts that parents will desert the current

reproductive attempt if the expected benefits of deserting are greater than the benefits of staying with the current attempt (Pianka 1976, Sargent and Gross 1985, Winkler 1991). The probability of desertion covaries with the proportion of the clutch removed, and greater losses result in higher desertion frequencies (Pianka 1976). In birds, nest desertion in response to partial clutch loss has been observed in species not exposed to brood parasitism (Winkler 1991, Delehanty and Oring 1993), species with intraspecific parasitism but no egg removal (Armstrong and Robertson 1988, Ackerman et al. 2003), and species with interspecific parasitism and egg removal (Rothstein 1982b). Because desertion in response to egg predation is prevalent across avian taxa, the hypothesis that desertion is a specific adaptation to brood parasitism must be examined carefully.

Bell's Vireo (*Vireo bellii*, hereafter 'vireo') is a good study species for investigating the cues that induce nest desertion because it is a cowbird host throughout its range, and vireo responses to cowbird parasitism vary among populations. Desertion of parasitized nests ranges from 29% ($n = 207$) in California where Least Bell's Vireos (*V. b. pusillus*) have been exposed to cowbirds for <200 years, to 74% ($n = 44$) in Kansas where the nominate subspecies (*V. b. bellii*) has been sympatric with cowbirds for millennia (Rothstein 1994, Kus 1999, Parker 1999). Nest desertion by vireos has been described as a specific response to cowbird parasitism because of three lines of evidence: most pairs fledge no young if a parasitic cowbird egg is accepted, parasitized nests are deserted more frequently than unparasitized nests, and pairs that desert one or more parasitized nests have higher productivity than pairs that accept cowbird eggs (Budnik et al. 2001, Kus 2002, Peer et al. 2005).

Our objective was to test two sets of hypotheses regarding nest desertion in Bell's Vireos. First, we sought to identify the cues that induce desertion. According to the 'anti-parasite

response hypothesis', nest desertion is a specific anti-parasite response to the presence of cowbird eggs. Under the 'egg predation hypothesis', nest desertion is a response to partial or complete clutch loss. The egg predation hypothesis is a refinement of the 'cowbird-induced desertion hypothesis', which predicts that desertion is a general response to cowbird activity, but not a specific anti-parasite behavior (Smith et al. 2003). Both hypotheses predict that vireos should desert nests where partial or complete clutch loss occurs, or if cowbirds replace host eggs with parasitic eggs after a delay (Table 2.1). The anti-parasite hypothesis predicts that vireos should desert if a cowbird egg is added to a natural nest, or if vireo eggs are replaced immediately by cowbird eggs in experimental nests. In contrast, only the egg predation hypothesis predicts that desertion is more likely if host eggs are removed prior to parasitism.

A second pair of hypotheses was developed to explain variation in frequency of desertion among breeding pairs. According to the 'intrinsic variation hypothesis', the consistent expression of response behaviors among vireo pairs is due to genetic or learned variation among pairs. In contrast, the 'environmental variation hypothesis' predicts that variation in nest contents, or exposure to the cue, creates multiple response behaviors among and within vireo pairs. The intrinsic variation hypothesis could be rejected if pairs both accepted and rejected parasitized nests within a breeding season, and pairs accepted a cowbird egg after deserting a previous parasitized nest (Table 2.2).

METHODS

Field Methods

We studied Bell's Vireos breeding at Konza Prairie Biological Station in northeastern Kansas, USA (39°05'N, 96°35'W) from 2003 to 2005. Male vireos arrived at the study site in the second week of May and established territories in areas with extensive shrub cover (primarily rough-

leaved dogwood, *Cornus drummondi*). Nest initiation started in late May and continued through July with all broods completing fledging by mid-August. Nests were located by searching territories in the vicinity of singing males. Females lay one egg per day, usually beginning within two days after the nest is completed, and modal vireo clutch size of unparasitized nests is four eggs. Vireo pairs in our study area frequently renest following predation or nest desertion, but produce one brood per year (Chapter 3). To quantify components of reproductive output, we monitored vireo territories and nests every three days to determine stage of the nesting cycle (construction, laying, incubation, or brood-rearing), nest contents including number of host and cowbird eggs, nest locations, and nest desertion frequency of vireo pairs.

Bell's Vireos are highly territorial, and use of discrete shrub patches made delineation of territories relatively easy. We were able to assign multiple nesting attempts to a pair in most territories. One challenge was that only 10 to 30% of territorial males were marked with color bands in each year. However, we were confident in assigning nests to unmarked birds because no marked male switched territories within a breeding season. Vireo pairs do not switch mates within a season, but may divorce and remate between years (Budnik et al. 2000). In addition, renesting occurred rapidly after failure and new nesting attempts were usually located a short distance away in the territory. Timing of nest loss on adjacent territories was rarely synchronous, so it was possible to distinguish among nesting attempts of adjoining pairs. Nests were checked every three days and we used the following criteria to classify the fate of nests. Cowbird eggs are large and brown-speckled and were easily distinguished from the smaller white vireo eggs. We classified a nest as 'parasitized' if it contained at least one cowbird egg, and considered a cowbird egg 'accepted' if vireos initiated incubation of a parasitized clutch. A nest was considered 'deserted' if the nest contents were cold and left unattended for

more than three days. Only two percent of all deserted nests did not contain cowbird eggs. We sometimes located a complete but empty nest that was actively defended by the pair, which, three days later, contained only cowbird eggs and was inactive. Even though we did not observe a vireo egg, these nests were considered deserted because cowbirds can remove host eggs and leave the nest empty, but vireos did not desert completed nests prior to laying an egg.

Timing of cowbird parasitism

To determine patterns of egg removal and laying by cowbirds, we monitored a subset of nests daily during the egg-laying stage in 2005. Nests were checked in the morning and again before sunset on the same day (day 1), in the afternoon on the following day (day 2), and again in the afternoon the next day (day 3). If a vireo clutch decreased on day 1, and contained an additional cowbird egg on day 2, we classified this as egg removal prior to parasitism. We determined that a cowbird removed an egg after parasitism when the clutch contents did not change on day 1, contained an additional vireo egg and a cowbird egg on day 2, and one fewer vireo egg on day 3.

Variation in intra-pair responses to parasitism

To examine intra-pair responses to parasitism within a season, we placed pairs that had two or more nests parasitized within a season into three categories based on response. 'Accepter pairs' accepted all parasitized nests, 'mixed-strategy pairs' accepted and deserted parasitized nests, whereas 'deserter pairs' deserted all parasitized nests.

Clutch manipulation experiments

To test if nest desertion was due to the presence of cowbird eggs or to egg loss, we manipulated unparasitized nests during laying. Pairs were used only once in this experiment, and we did not include nesting attempts of manipulated pairs in other analyses. Manipulations were performed after 09:00 h CST on the day the third vireo egg was laid to mimic the time of day when female

cowbirds remove host eggs (K.L. Kosciuch pers. obs., Sealy 1992). We used two cowbird eggs in each manipulation because multiple parasitism is more common than the addition of a single cowbird egg at our study site (56% of parasitized nests; K.L. Kosciuch unpubl. data). Our design enabled us to evaluate a realistic scenario of egg loss while controlling for the number of cowbird eggs added to a nest. Cowbird eggs used in this experiment were obtained from deserted vireo nests or nests of other songbird hosts, and were marked for identification. Although 100% of the vireo clutch can be removed by cowbirds during parasitism at our study site, we removed only a portion of the vireo clutch because total egg loss usually leads to nest desertion. We expected that vireos might be more tolerant of clutch reduction later in the breeding season given that opportunities for renesting were reduced. Thus, we conducted all manipulation experiments prior to 1 July because a majority of nests (>95%, $n = 542$) were initiated before this date.

We conducted three clutch manipulation treatments: control, exchange, and removal. In all treatments, we handled vireo eggs with a small measuring spoon to avoid damaging other eggs in the clutch. In 'control' treatment, we removed two vireo eggs from the nest and then immediately returned them. Handling of eggs controlled for observer and disturbance effects on nest desertion. In 'exchange' nests, we removed two vireo eggs and immediately replaced them with two cowbird eggs. In 'removal' nests, we removed two vireo eggs and replaced them with two cowbird eggs the next morning before 07:30 h CST. After experimental treatment, vireo nests were monitored daily until the response of the attending pair was determined. The nest was considered 'attended' if the pair laid another egg or initiated incubation. The nest was considered 'deserted' if the eggs were cold and the pair was not attentive for three consecutive visits, or if the pair initiated a new nest elsewhere. We did not place a mounted female cowbird

at the nest prior to the clutch manipulations because the presence of even a live cowbird at the

nest does not appear to cause vireos to desert (Sharp and Kus 2004).

Statistical analyses

To determine which factors influenced nest desertion, we used generalized linear models with a

binomial error distribution and a logit link (PROC GENMOD in SAS). We used three predictor

variables: number of vireo eggs remaining, number of cowbird eggs received, and total number

of host and parasitic eggs. We also substituted parasitism status (parasitized or unparasitized) for

number of cowbird eggs received. Model selection was based on Akaike Information Criterion

values corrected for small sample size (AIC_c):

$$AIC_c = \text{Dev} + 2K + \frac{2K(K+1)}{(n-K-1)}$$

where Dev is the model deviance (-2ln*L*), *K* is the number of parameters in the model, and *n* is

the sample size. The model with the lowest AIC_c value was considered the most parsimonious

model ($\Delta AIC_c = 0$), and any additional models with ΔAIC_c values ≤ two were considered equally

parsimonious. If two models differed by only one parameter and ΔAIC_c was ≤ 2, we examined

model deviance to determine if the inclusion of the extra parameter explained additional

variation in the response (Guthery et al., 2005). We calculated Akaike weights (w_i) to determine

the strength of support for each candidate model:

$$w_i = \frac{e^{(-\Delta_i/2)}}{\sum_{r=1}^{R} e^{(-\Delta_r/2)}}$$

where Δ_i is the ΔAIC_c value of the selected model relative to the sum of all candidate models

(Δ_r). The ratio of Akaike weights for the best fit model and other models in the candidate set

was used to determine the relative support among models. We checked the fit of the top model

by using the Hosmer-Lemeshow test and concluded the model was a good fit to the data if $p >$ 0.05. We estimated effects (β) in the best model ($\Delta AIC_c = 0$) using a mixed-effects logistic regression, including the variable 'pair' as a random effect (GLIMMIX macro for PROC MIXED). We attempted to conduct model selection using this method, but some complex models would not converge when random effects were included. The desertion probabilities we report from the mixed-effects logistic regression model control for the inclusion of multiple nests per pair in our analysis. We interpreted the direction and strength of the effect from the odds ratios (e^{β}). An odds ratio > 1 indicates that the treatment increased the odds of an event, whereas an odds ratio < 1 indicates the opposite.

We used a general linear mixed model (PROC MIXED) to test for differences among vireo pair response categories for the mean number of vireo eggs that remained in a parasitized nest and the mean number of cowbird eggs received. Nests were classified as those of accepter pairs, deserter pairs, and mixed-strategy pairs. Nests from mixed-strategy pairs were sub-divided into accepted nests and deserted nests. We included pair as a random effect to account for the non-independence of nests within a category. We used Levene's test to examine homogeneity of variances among response categories for each dependent variable. Although our data were not normally distributed, they were skewed in the same direction and our sample size was large for each category. The *F*-test is robust against departures from normality under these conditions; therefore, we did not transform the data (Lindman 1974). We used Tukey's test for multiple comparisons to determine which group(s) differed. We did not include data from nests that were depredated before we could determine the pairs' response or data from pairs for which we were not confident that we located all nesting attempts within a season. All data are presented as frequencies or means ± SE and statistical tests were conducted with a two tailed $\alpha = 0.05$.

RESULTS

Nest desertion in unmanipulated nests

The proportion of nests that were deserted increased as 2 or fewer vireo eggs remained in the nest (Fig. 2.1). Nests that contained zero vireo eggs ($n = 145$) were deserted 100% of the time, regardless of the number of cowbird eggs the nest contained. Nests that contained three or four vireo eggs ($n = 243$) were not deserted even if as many as three cowbird eggs were added. When two vireo eggs ($n = 35$) remained, the proportion of nests deserted increased as a function of the number of cowbird eggs received.

The top logistic regression model ($\Delta AIC_c = 0$) was a good fit to the data ($\chi^2_8 = 10.92$, $P = 0.21$) and contained two factors: the number of vireo eggs remaining and number of cowbird eggs received (Table 2.3). Models that contained number of vireo eggs received > 99% of the support among candidate models. In contrast, models that contained number of cowbird eggs added received a total of 62% of the support, and models that contained parasitism status received a total of 17% of the support. Single factor models that contained parasitism status, number of cowbird eggs received, and total eggs received little support ($\Delta AIC_c > 300$, $w_i < 0.01$; Table 2.3). In contrast to the weak predictive power of the number of cowbird eggs received or parasitism status alone, the number of vireo eggs remaining in a nest was a strong predictor of nest desertion ($w_i = 0.21$, $\Delta AIC_c = 2.1$).

When we included the terms from the top logistic regression model in a mixed-effects logistic regression, we found that pair was a significant random effect ($z = 8.14$, $P < 0.0001$), possibly because the intensity of parasitism varied among territories. Including pair as a random effect, the logistic equation was:

Logit $(p) = 4.51 - 2.47$ (vireo eggs remaining) $+ 0.34$ (cowbird eggs received)

The negative β estimate for vireo eggs remaining indicates that the probability of desertion decreased as the number of vireo eggs in a nest increased. Controlling for the number of cowbird eggs in a nest, each loss of a vireo egg increased the odds of nest desertion by 11.8× (95% CI = 6.5, 18.4). The positive β estimate for cowbird eggs received indicates that the probability of desertion increased as the number of cowbird eggs in a nest increased. Controlling for the number of vireo eggs remaining in a nest, each addition of a cowbird egg increased the odds of nest desertion by 1.4×, but the 95% CI surrounding the odds ratio included one (0.53, 3.27).

Timing of cowbird parasitism and egg removal

In our subset of nests monitored daily, we found that when cowbirds parasitized a vireo nest, they removed a vireo egg prior to parasitism, after parasitism, or in some cases, not at all (Table 2.4). Vireos deserted 100% of the nests when cowbirds removed all of the vireo eggs prior to parasitism, regardless of clutch size prior to removal. As the proportion of the total clutch removed prior to parasitism decreased, so did the proportion of nests deserted (Table 2.4). Vireos did not desert nests when cowbirds removed an egg within two days after parasitism, even when 50% of the total clutch and 100% of the vireo clutch was removed. Egg removal by cowbirds occurred prior to parasitism ($n = 10$) more often than after parasitism ($n = 4$), but the difference was not significant in our small sample ($z = 0.11$, $P = 0.27$). We found that the number of vireo eggs removed and the number of cowbird eggs received were positively correlated among nests monitored daily ($r = 0.64$, $P = 0.006$, $n = 16$).

As a comparison with the effects of cowbird egg removal during egg laying, we examined effects of natural partial clutch removal during incubation. Vireos deserted 63% ($n = 8$) of the nests when less than 25% of the clutch was removed during incubation, 82% ($n = 12$) of

the nests when 25% to 50% of the clutch was removed, and 100% of the nests ($n = 25$) when >50% of the clutch was removed.

Clutch manipulations

Vireos deserted no control nests ($n = 10$), and no exchange nests where two of three vireo eggs were immediately exchanged for cowbird eggs ($n = 7$). However, 83% of removal nests were deserted when two of three vireo eggs were removed the night before the cowbird eggs were added ($n = 6$). Overall, removal nests were significantly more likely to be deserted than exchange or control nests combined (Fisher's Exact Test, $P \leq 0.005$).

Variation in intra-pair response to parasitism

Of monitored vireo pairs ($n = 88$), 11% were consistently accepter pairs and 32% were consistently deserter pairs. The remaining 57% were mixed-strategy pairs. Of these mixed-strategy pairs, significantly more (76%, $n = 50$) deserted a parasitized nest before accepting a cowbird egg than accepted a cowbird egg before deserting a parasitized nest (McNemar's test, exact p-value < 0.001).

Variances did not differ among response categories for the number of cowbird eggs added (Levene's test, $F_{3, 262} = 0.76$, $P = 0.52$), or for the number of vireo eggs that remained ($F_{3, 262} = 1.85$, $P = 0.14$). The mean number of cowbird eggs received per nest differed among responses ($F_{3, 171} = 9.42$, $P < 0.0001$; Figure 2.2a). Nests accepted by mixed-strategy pairs contained fewer cowbird eggs than deserted nests of mixed-strategy pairs or the nests of deserter pairs. However, the number of cowbird eggs in the nests of accepter pairs did not differ from the number of cowbird eggs in the nests of deserter pairs. The mean number of vireo eggs that remained in a parasitized nest also differed among responses ($F_{3, 262} = 249.3$, $P < 0.0001$; Figure 2b). Nests that were accepted contained more vireo eggs than nests that were deserted.

DISCUSSION

Desertion of parasitized nests by Bell's Vireos was explained by the egg predation hypothesis, and variability in desertion could be attributed to variation in nest contents. Egg loss induced nest desertion, and we reject the anti-parasite hypothesis because three core predictions were not upheld. First, vireos regularly accepted cowbird eggs. If nest desertion was a specific response to parasitism, then our top logistic regression model should have included parasitism status (presence or absence of cowbird eggs) because vireos incur reproductive failure if they accept even one cowbird egg. Further, vireos deserted removal nests, but not experimental exchange nests and rarely deserted naturally parasitized nests if cowbird laying occurred before host egg removal. Hosoi and Rothstein (2000) suggested that the presence of a cowbird at the nest likely caused desertion in many non-forest species because experimentally parasitized nests are rarely deserted. Our results demonstrate that egg removal by cowbirds is another mechanism that can cause desertion in a species that does not respond to the presence of cowbird eggs. We unambiguously rejected the intrinsic variation hypothesis in favor of the environmental variation hypothesis for explanation of variation in nest desertion among and within pairs. Environmental variation, in the form of extent of host egg loss, explained nearly all the variation in desertion of parasitized nests. The intrinsic variation hypothesis was not supported because most pairs both accepted and deserted parasitized nests, and there was no evidence that pairs learned to desert parasitized nests.

The only evidence in support of a role for the presence of cowbird eggs in nest desertion behavior by Bell's Vireos was from nests that contained two vireo eggs. In that case only, we saw a positive relationship between number of cowbird eggs laid and probability of nest desertion. However, in vireo nests with two eggs remaining, between zero and three vireo eggs could have been removed. Further, our daily nest checks showed a strong correlation between the

number of host eggs removed and the number of cowbird eggs laid. Thus, the apparent cowbird egg effect in two-egg vireo nests is instead likely due to cowbird removal of vireo eggs.

The observation that Bell's Vireos desert nests in response to egg loss supports the predictions of parental investment theory. Vireos breeding in our study region can renest up to six times within a season (Chapter 3, Budnik et al. 2001). The expected benefits of deserting a partially depredated clutch are likely greater than the benefits of attending the clutch because vireos have opportunities to renest. Renests are less likely to be parasitized because parasitism frequency decreases throughout the season in this region (Parker 1999, Budnik et al. 2001). However, the seasonal effects of date of clutch initiation on post-fledging survival of juveniles are unknown. We conclude that nest desertion by Bell's Vireos at our study site is a general response to egg predation. It only appears to be a specific anti-parasite behavior because vireos desert parasitized nests at high frequencies.

Two hypotheses have been proposed to explain the absence of specific adaptive response behaviors by host species to brood parasites (Rothstein 1975, 1990, Rowher and Spaw 1988, Lotem et al., 1992). The 'evolutionary equilibrium' hypothesis suggests host species have not evolved anti-parasite behaviors because the costs of rejection are greater than acceptance (Rowher and Spaw 1988, Lotem and Nakamura 2000). The cost of acceptance of parasitic eggs in Bell's Vireos is certain nest failure unless the cowbird egg fails to hatch or is laid during vireo incubation (K.L. Kosciuch pers. obs). Because losses of productivity clearly outweigh the potential costs of rejection, the evolutionary equilibrium hypothesis can be rejected for vireos. The 'evolutionary lag' hypothesis posits that species recently exposed to brood parasitism do not respond adaptively due to temporal constraints on the evolution of new genetic variants (Mayfield 1965, Rothstein 1975). Lag is often a presumed explanation after a species is found to

accept parasitic eggs but suffers high fitness costs (e.g., Graham 1988, Ward et al. 1996, Whitehead et al. 2002, Johnson and van Riper 2004).

Three mechanisms may be responsible for evolutionary lag in vireos. First, although cowbirds and vireos (*V. b. bellii*) have been sympatric for millennia in the Great Plains, recent exposure may have increased if fire suppression and shrub expansion have brought *V. b. bellii* into greater contact with cowbirds in tallgrass prairie. Second, gene flow among *V. b. bellii* populations that vary in exposure to parasitism could also hamper adaptation in local populations. Jensen and Cully (2005) found pronounced spatial variation in that parasitism frequency of grassland birds with high rates in the Flint Hills region of northeastern Kansas near our study area, and low rates in the southern Flint Hills. Vireos from populations parasitized at lower frequencies would not have to disperse long distances to reach our study population. Last, the generalized nest desertion response could reduce the strength of selection imposed by cowbirds on vireos, and thus make an anti-parasite response to cowbird parasitism less likely to evolve. However, this situation may be uncommon elsewhere in the vireos' breeding range due to the unusually high cowbird density and associated high frequency of nest desertion at our study site.

The environmental variation hypothesis was sufficient to explain variation in nest desertion among pairs of vireos in Kansas, and may also account for variability in desertion frequencies among vireo populations. Vireos in Kansas desert parasitized nests at a higher rate than the Least Bell's Vireo (*V. b. pusillus*) in California. There is a 40-fold difference in cowbird density between our study area in northeastern Kansas compared to Kus' (1999) study area in southern California. Based on route level analyses of Breeding Bird Survey data (1989 to 1998), 162.4 and 216.3 cowbirds per 100 km surveyed were detected on two routes near our study area

in Kansas (routes 38016, 38019), whereas only 5.2 and 5.7 cowbirds per 100 km surveyed were

detected on two routes (14119, 14120) near the study area in southern California (Sauer et al.

2005). Nest disturbance, parasitism frequency, and rates of multiple parasitism per nest are

correlated with female cowbird abundance (Jensen and Cully 2005), and we suggest that nest

desertion frequency is likely to be higher in Kansas because nests are often parasitized multiple

times and thus suffer higher rates of egg removal by cowbirds early in the vireo egg laying stage.

The environmental variation hypothesis may explain similar patterns of spatial variability in

desertion frequencies in other species, such as Willow Flycatcher (*Empidonax traillii*, Hosoi and

Rothstein 2000).

Understanding the causes of variation in nest desertion has important implications for

management of songbirds of conservation concern. If phenotypic variation in desertion is

primarily environmental rather than genetic, then managing a population in an attempt to allow

selection to increase the prevalence of the behavior might be misguided. For example,

decreased population density and low productivity of the federally endangered Least Bell's Vireo

have been attributed to loss of breeding habitat, and losses to cowbird parasitism (Kus 1998,

1999). Cowbird trapping is a well-established management tool, and cowbird removals have

increased productivity, population growth, and density of *V. b. pusillus* (Kus 1999, Griffith and

Griffith 2000, Kus and Whitfield 2005). Recently, Peer et al. (2005) suggested relaxing the

trapping effort to renew selection pressures and facilitate the evolutionary spread of a desertion

response, a behavior assumed to be present in *V. b. bellii*. We have demonstrated that despite

high fitness costs and high desertion frequencies, *V. b. bellii* in Kansas do not respond adaptively

to the presence of cowbird eggs, and that variation in desertion is determined by variation in host

egg number. Thus, it is unlikely that reducing cowbird control in California will facilitate the

evolution of anti-parasite behaviors in time scales relevant to management objectives because vireos do not possess explicitly anti-parasitic behaviors. Thus, it is critical to understand the proximate mechanisms that cause nest desertion when developing management strategies for songbirds of conservation concern.

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Table 2.1 Predicted behavior of Bell's Vireo if nest desertion is due to an anti-parasite response or a generalized response to egg predation.

	Behavior consistent with	
Vireo behavior	Anti-parasite response	Egg predation response
Desert if one or more cowbird eggs are added	Yes	No
Desert if partial or complete clutch loss occurs	Yes	Yes
More likely to desert if vireo eggs are removed prior to parasitism	No	Yes
Desert if vireo eggs are immediately replaced by cowbird eggs	Yes	No
Desert if vireo eggs replaced by cowbird eggs after at least a 12 hour delay	Yes	Yes

Table 2.2 Predicted behavior of Bell's Vireo if variation in nest desertion response is due to intrinsic (genetic or learned) or environmental (cue) variation.

Vireo behavior	Intrinsic variation	Environmental variation
Breeding pairs commonly both accept and desert parasitized nests within a season	No	Yes
Breeding pairs accept cowbird eggs in a renesting attempt after deserting a parasitized nest	No	Yes
Larger change in cue (host or cowbird eggs) intensity more likely to cause desertion	No	Yes

Table 2.3 Logistic regression model results for the probability of nest desertion for Bell's Vireos in relation to the number of cowbird eggs received (0–4, CE), the number of vireo eggs remaining (0–4, VE), parasitism status (parasitized by one or more cowbird eggs or unparasitized, PS), and total number of eggs in the nest (1–6, TE).

Factors	Model statistics[a]				
	AIC_c	ΔAIC_c	K	deviance	w_i
VE, CE	59.6	0.0	3	53.6	0.62
VE	61.8	2.1	2	57.8	0.21
VE, PS	62.2	2.6	3	56.2	0.17
TE	324.0	264.3	2	319.9	0.00
CE	503.2	443.6	2	499.2	0.00
PS	532.1	472.4	2	528.1	0.00

[a]AIC_c is the Akaike Information Criterion (AIC) value corrected for small sample size,

ΔAIC_c is the difference between subordinate models and the top model ($\Delta AIC_c = 0$),

and w_i is the Akaike weight.

Table 2.4 Timing of Bell's Vireo egg removal by Brown-headed Cowbirds in Kansas based on repeated daily observations of parasitized unmanipulated nests found during building or egg laying.

Timing of vireo egg removal[a]	% total clutch removed	% vireo clutch removed	No. nests	No. deserted
Prior to parasitism	> 50	> 50	8	8
Prior to parasitism	≤ 50	≤ 50	2	0
After parasitism	≤ 50	> 30	4	0
No removal	0	0	2	0

[a]Vireo eggs removed prior to parasitism were removed by cowbirds the day before a

cowbird laid an egg in the nest. Vireo eggs removed after parasitism were removed

by cowbird either the day of cowbird laying or the following day.

Figure 2.1 Percent of nests deserted in relation to natural variation in the number of vireo eggs remaining and cowbird eggs received. Sample size of nests for each combination of vireo and cowbird eggs at the end of laying are listed above the x-axis.
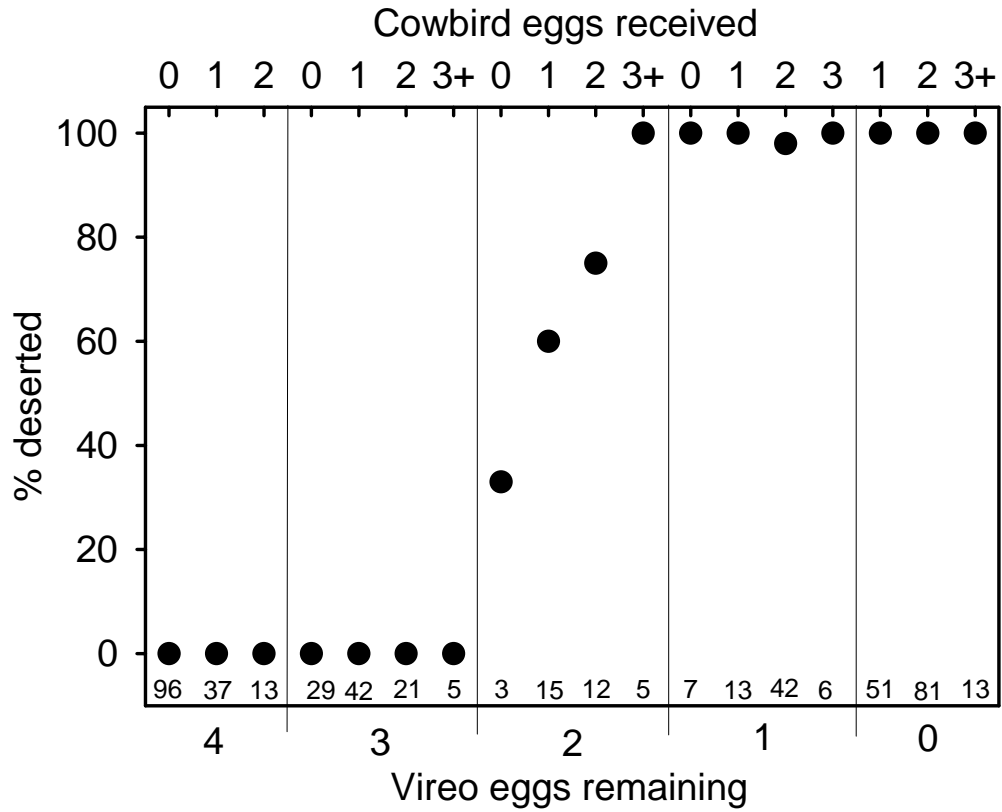
Figure 2.2 Mean (± SE) number of eggs in a Bell's Vireo nest based on the response of the pair to parasitism by Brown-headed Cowbirds. Only pairs that had two or more nests parasitized within a season were included in this analysis. (a) Number of Brown-headed Cowbird eggs received in Bell's Vireo nests; (b) number of vireo eggs that remained in parasitized nests. Accepter pairs accepted cowbird eggs in all nests, mixed-strategy pairs both attended and deserted parasitized nests within a season, and deserter pairs deserted all parasitized nests. Mixed-strategy pairs are partitioned into nests where cowbird eggs were accepted and nests that contained cowbird eggs and were deserted. Number of nests is inside the bars. Bars with the same letter are not significantly different ($p > 0.05$).
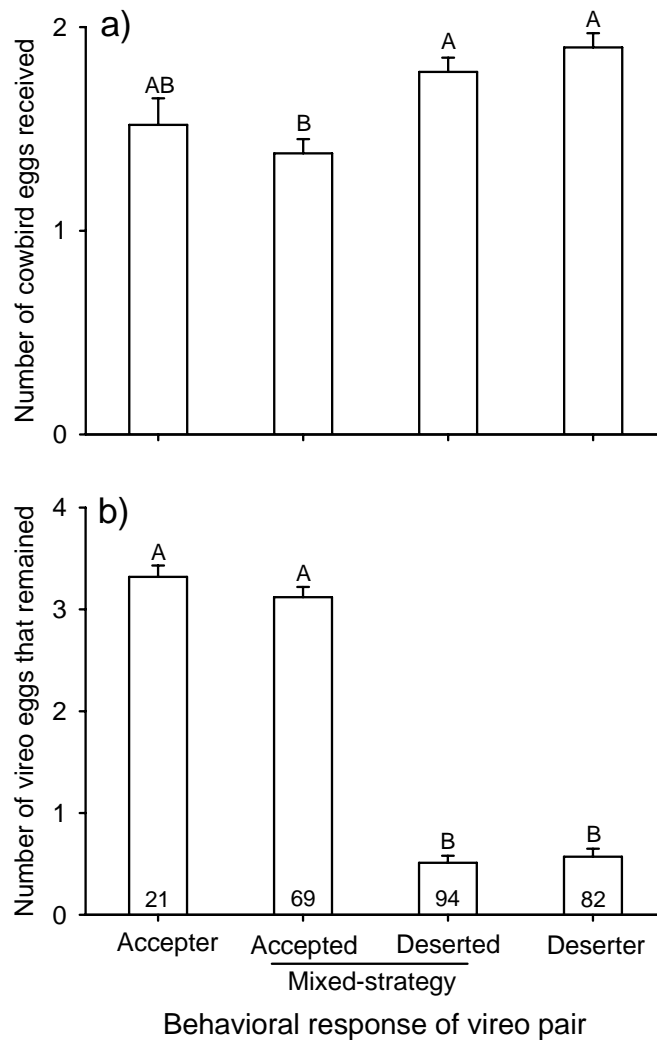
CHAPTER 3 - EXPERIMENTAL COWBIRD REMOVAL INCREASES HOST AND PARASITE PRODUCTIVITY

Karl L. Kosciuch and Brett K. Sandercock

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 switch-back experimental design. Cowbird removals decreased parasitism frequency from 77% on unmanipulated plots to 58% on cowbird removal plots, and vireo productivity per nest was higher on cowbird removal plots (mean vireo fledglings per nest = 1.1 ± 0.1SE, $n = 130$ nests) than on unmanipulated plots (mean = 0.4 ± 0.05, $n = 278$). Nest desertion frequency was lower on cowbird removal plots (35%) compared to unmanipulated plots (69%), because removal of host eggs was the cue for nest desertion, and vireos experienced lower rates of egg loss on cowbird removal plots. Parasitized nests failed more frequently than unparasitized nests, but failure rates of parasitized nests did not differ between experimental treatments, and the probability of failure was > 0.65 for parasitized nests overall. Unexpectedly, cowbird productivity from vireo nests was higher on cowbird removal plots (mean cowbird fledglings per vireo nest = 0.10 ± 0.03, $n = 278$ nests) than on unmanipulated plots (0.06 ± 0.01, $n = 130$) because fewer parasitized nests were deserted. Overall, cowbird removal substantially increased vireo productivity, and our results for the host species are consistent with results from other cowbird removal studies. However, our study demonstrates that increases in cowbird productivity can be an unintended consequence of

cowbird removals. Thus, the overall effects of cowbird removal on host and parasite

demography should be evaluated with community-wide studies.

INTRODUCTION

The effects of interspecific brood parasitism on productivity differ among avian parasites and

their hosts. The nestlings of European Cuckoos (*Cuculus canorus*), and honeyguides (Family

Indicatoridae) cause complete host reproductive failure because parasitic young regularly eject

host eggs or nestlings, or kill nest mates (Friedmann 1955, Davies and Brooke 1989). Despite

potentially high costs of parasitism, cuckoos, honeyguides, and other host-specific brood

parasites may have little population level effects on host species because parasites occur at low

densities. Generalist brood parasites such as the Brown-headed Cowbird (*Molothrus ater*;

hereafter 'cowbird') do not depend on a single host species and routinely parasitize a large

number of host species (Rothstein 1975). Therefore, cowbirds can be more abundant than some

host species and cowbird parasitism can cause large reductions in host productivity because the

extirpation of an uncommon host is unlikely to affect population viability of cowbirds.

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 more food than host nestlings

(Lichtenstein and Sealy 1998, Kilner et al. 2004). Female cowbirds directly reduce host

productivity by removing host eggs prior to or following parasitism (Sealy 1992), and may

destroy the contents of nests during incubation brood-rearing to induce hosts to renest ('cowbird

predation hypothesis', Arcese et al. 1996, Elliott 1999, Granfors et al. 2001). Species-specific

costs of parasitism may also be influenced by host life history traits, 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 are difficult to evaluate because applied studies neglected to monitor host productivity in reference areas where cowbirds were not removed (Griffith and Griffith 2000, Kus and Whitfield 2005). 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 cowbird trapping to aid in the recovery of songbird species has been challenged because control programs may direct funds away from habitat restoration, have rarely been discontinued, and kill thousands of cowbird annually (Rothstein and Peer 2005). For example, cowbird removals are one component of management efforts for the endangered Least Bell's Vireo (*Vireo bellii pusillus*) in California and the Black-capped Vireo (*Vireo atricapilla*) in Texas, and removals have been conducted since the 1980s at most study areas (Kostecke et al. 2005, Kus and Whitfield 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 effects of cowbird removals on songbird population demography. Three studies lacked unmanipulated reference sites and are effectively uncontrolled experiments (DeCapita 2000, Kostecke et al. 2005, Kus and Whitfield 2005). Two studies had reference sites, but one addled cowbird eggs in

control and cowbird removal areas, making assessment of cowbird removals alone difficult (Whitfield 2000, Morrison and Averill-Murray 2002). The best study to date examined the effects of cowbird removals on Song Sparrow (*Melospiza melodia*) demography (Smith et al. 2002, Smith et al. 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 would provide valuable data for the management of species of conservation concern. Moreover, spatial and temporal variation in cowbird densities and parasitism rates often occurs on a regional scale, and removal experiments are needed to determine how these factors interact to influence the regional costs of parasitism for host species (Jensen and Cully 2005b). In this study, we conducted a cowbird removal experiment in an area with high parasitism frequencies (> 80% of nests for preferred host species) to evaluate the effects of cowbird parasitism and cowbird control on the productivity of a Great Plains population of Bell's Vireo (*V. b. bellii*, hereafter 'vireo').

Our objective was to determine if parasitism by cowbirds can limit the productivity of a small-bodied songbird. At a landscape scale, 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 on cowbird removal plots. Nest desertion by small-bodied hosts can reduce the costs of parasitism, and Parker (1999) found that 75% of the parasitized vireo nests at our study site were deserted. However, nest desertion in vireos is a generalized response to egg removal by predators and not due to the addition of cowbird eggs (Chapter 2). 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 desertion of parasitized nests would be less likely on removal plots because more vireo eggs would remain in parasitized nests at the end of the vireo laying period. Decreased vireo productivity in the presence of cowbirds is due to a high probability of failure when even one cowbird egg is accepted (Parker 1999, Budnik et al. 2001, Kus and Whitfield 2005). Another possible link between cowbirds and decreased vireo productivity could result from female cowbirds destroying vireo nests to induce renesting by hosts. 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 at our study site, then the probability of nest success for parasitized nests would be lower than unparasitized nests, and we predicted that parasitized nests on unmanipulated plots should have a lower probability of success than parasitized nests on removal plots. Cowbird removals typically increase the proportion of nests on the landscape that are unparasitized and reduce the number of cowbird eggs per nest (Smith et al. 2002). Thus, we expected that cowbird productivity and density to be positively correlated, and predicted that cowbird productivity from vireo nests would be higher on plots where cowbirds were not removed.

METHODS

Study site and cowbird removal

Our study was conducted from 2003–2005 at the 3,487 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 approximately 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-grazed (*Bos taurus*), bison-grazed (*Bos bison*), or ungrazed. 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 (see Hartnett et al. 1996 for a complete site description).

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. 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 ($1.8 \times 1.5 \times 1.8$ 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. 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 non-target species. Surplus cowbirds were removed from traps with hand-held nets and euthanized by cervical dislocation when traps contained more than 20 individuals.

In 2005, we conducted variable width line transect surveys on removal (KP3, KP4) and unmanipulated plots (KP1, KP2) to estimate cowbird density. A 500 m transect was placed through the center of the plot and surveyed twice two weeks prior to cowbird removal (early = 1st week of May) and twice two weeks prior to the termination of trapping (late = 2nd week of July).

Radial angle, distance (m), number of individuals, and sex were recorded for all cowbirds observed during morning visits.

Vireo reproduction and response to parasitism

Bell's Vireos are an obligate shrub-nesting species that have well-defined territories at Konza Prairie (Parker 1999, Chapter 2). 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 (CST) 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% to 30% of the males were uniquely color-banded each year. No color-banded male switched territories within a season (K.L. Kosciuch, unpubl. data). 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, K.L. Kosciuch, pers. obs.). 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 approximately 14 days and provision the brood for about 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 over 30

days after the young leave the nest. Although vireos frequently renested following nest failure, a maximum of only raised one brood per year at our study site.

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. Vireo eggs are white with sparse spotting and were easily distinguished from the larger cowbird eggs with abundant brown spotting. We determined that cowbird eggs were 'accepted' if the pair initiated incubation of a parasitized clutch. If the eggs were cold and the nest was left unattended for at least three days, we considered the nest to be 'deserted'. If a portion of the clutch or 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

Cowbird density estimates

To determine if cowbird removals reduced cowbird densities, we estimated densities in Program Distance (5.2). We used the half-normal detection function and the cosine, simple polynomial, and hermite polynomial series expansions. Model selection was based on Akaike Information Criterion values (AIC). The model with the lowest AIC value was considered the most parsimonious model (ΔAIC = 0) and additional models with ΔAIC values ≤ 2 were considered equally parsimonious. Density estimates were derived from the model with the lowest ΔAIC value and best fit based on the Kolmogorov-Smirnov test. We pooled sexes for density estimates

because sample size of females was limited. Density estimates are density (individuals per ha) ±

SE.

The effects of cowbird removal on parasitism and vireo desertion response

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 between plots within treatments for

subsequent analyses because probability of parasitism and nest desertion did not differ among

plots (see RESULTS). To test our hypothesis regarding the effects of cowbird removal, we

limited our analyses to data from 2004 and 2005.

To model the probability of parasitism and desertion of parasitized nests, we used logistic

regression (PROC GENMOD) in Program SAS and included data from nests that received at

least one vireo or cowbird egg. A set of *a priori* candidate models, which contained factors we

believed to have influenced variation in the response variable was developed prior to analysis.

Candidate models for the probability 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; Morrison and Averill-Murray 2002), and week of clutch initiation

(to control for seasonal declines in parasitism; Parker 1999). We set week $1 = 9 - 16$ 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 indicated that the factor increased

the odds of an event, whereas odds ratios < 1 indicates 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 effects 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 2005b). 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 than productivity per nest because population growth models are based on the seasonal fecundity of females. Productivity per nest fails to account for variation in number of renesting attempts (Pease and Grzybowski 1995, Grzybowski and Pease 2005). However, we report both metrics because most past studies have monitored unmarked birds and many report 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. We included the factor parasitism status (parasitized or unparasitized) because we did not expect cowbird removal to affect the number of vireo eggs in unparasitized nests. 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 and included all nests that received at least one egg. We did not

use nest survival models because most nests were found during nest construction. Although

vireos usually fail to fledge young from parasitized nests, we considered nests that fledged only

cowbirds successful because the nest escaped predation and produced young. Because models

that contain data from all nests with at least one egg include losses to abandonment during egg

laying, we used logistic regression to model the probability of nest success during incubation and

brood rearing. Egg removal by cowbirds during the vireo laying cycle causes nest desertion

(Chapter 2), and while this constitutes an act of predation, we were also interested in losses to

predation past the primary stage of cowbird activity. To determine if the probability of failure of

parasitized nests is higher on 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 vireo productivity and cowbird

productivity from vireo pairs, we calculated the effect size (Hedge's *d*) and the variance of the

effect size for each year (Gurevitch and Hedges 1999). We calculated effect sizes for Song

Sparrows (*Melospiza melodia*) productivity and cowbird productivity per Song Sparrow pair,

(Smith et al. 2002) to examine interspecific variation in the effects of cowbird removal on host

and parasite productivity.

RESULTS

Cowbirds captured and density estimates

We captured and removed a similar number of female cowbirds in each year at all removal plots combined (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 were similar in both years (2004: $n = 39$; 2005: $n = 46$).

The top model for cowbird density contained a half-normal detection function and simply polynomial series expansion, and was a good fit to the data (ΔAIC of next best model = 1.38, Kolmogrov-Smirnov test = 0.22, $P = 0.45$). Cowbird densities declined seasonally from 1.56 ± 0.51 SE to 0.94 ± 0.28 individuals per ha on unmanipulated plots, and from 1.34 ± 0.43 to 0.52 ± 0.23 individuals per ha on cowbird removal plots. Despite removing substantial number of cowbirds, density estimates decreased by only 61% on removal plots compared to 40% on unmanipulated plots during the sampling period, and estimates of density did not differ significantly when we compared treatments in either sampling period (early: $t_{35} = -0.35$, $P = 0.70$; late: $t_{24} = 1.15$, $P = 0.26$).

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 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 ($\chi^2_3 = 1.71$, $P = 0.63$, Fig. 3.1). Thus, we pooled plots within treatments for subsequent analysis.

Experimental cowbird removals reduced parasitism frequency in both removal years from an average of $77 \pm 0.6\%$ SE ($n = 139$) on unmanipulated plots to $58 \pm 0.8\%$ ($n = 69$) on cowbird removal plots in 2004, and from an average of $85 \pm 0.6\%$ ($n = 139$) on unmanipulated plots to $47 \pm 0.8\%$ ($n = 61$) on cowbird removal plots in 2005 (Fig. 3.1). We did not find a carry-over effect of cowbird removal on parasitism frequency when we compared KP1 ($\chi^2_1 = 1.72$, $P = 0.19$) or KP2 to KP5 ($\chi^2_1 = 0.36$, $P = 0.55$) in 2005, suggesting that both plots experienced parasitism frequencies similar to unmanipulated plots after cowbird trapping was discontinued. Our global model for the probability of parasitism was a good fit to the data ($\chi^2_8 = 10.3$, $P = 0.25$). The top two models in our candidate set received 93% of the support (Table 3.1). The top model contained week of clutch initiation and treatment, and garnered 56% of the support among the candidate models. The model that contained the factor year had a ΔAIC_c value < 2, but the inclusion of year lead 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 on unmanipulated plots were $5.0\times$ (95% CI = 3.0, 8.3) greater than the odds of parasitism on removal plots. The odds of parasitism decreased 28% per week over the course of the breeding season. The probability of parasitism in week one on a removal plot (0.77; 95% CI = 0.66, 0.85) was similar to the probability of parasitism in week six on an unmanipulated plot (0.77; 95% CI = 0.71, 0.82; Fig. 3.2A).

Parasitism frequency was positively correlated with parasitism intensity ($r = 0.73$, $P = 0.003$, $n = 14$), and lower rates of multiple parasitism were found on removal plots (2004: 35 ± 1.8 SE %; 2005: $33 \pm 0.9\%$) than unmanipulated plots (2004: $58 \pm 0.4\%$; 2005: $58 \pm 0.6\%$; Fig. 3.1). Week and treatment explained significant variation in the mean number of cowbird eggs

per parasitized nest. Parasitized nests on unmanipulated plots contained 0.38 more cowbird eggs per nest on average than parasitized nests on cowbird removal plots ($F_{1, 268} = 9.4$, $P < 0.001$; Table 3.2). The mean number of cowbird eggs per parasitized nest decreased by approximately 0.06 cowbird eggs per nest per week throughout the season ($F_{1, 268} = 7.9$, $P = 0.005$).

Desertion frequency of parasitized nests was positively correlated with parasitism frequency ($r = 0.84$, $P < 0.001$, $n = 14$), and lower rates of nest desertion were found on removal plots (35 ± 0.5% SE) compared to unmanipulated plots (69 ± 0.5%; Fig. 3.1). Our global model for the probability of nest desertion was a good fit to the data ($\chi^2_8 = 1.97$, $P = 0.98$). The top model contained treatment and week of clutch initiation, and garnered 48% of the support among the set (Table 3.1). 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× 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 on unmanipulated plots were 4.9× (95% CI = 2.7, 9.1) greater than the odds of desertion on removal plots. The odds of desertion decreased 13% per week over the course of the breeding season. The probability of desertion in week one on a removal plot (0.45; 95% CI = 0.30, 0.61) was lower than the probability of desertion in week nine on an unmanipulated plot (0.57; 95% CI = 0.39, 0.72; Fig. 3.2B).

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 to 3.8 eggs per plot (Table 3.2). In contrast, the mean number of vireo eggs in parasitized nests was approximately 0.7 to 1.3 eggs greater on

removal plots in 2004 and 2005 (Table 3.2). 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 3.2).

We found a significant interaction between treatment and parasitism status for the probability of nest success when we used data from all nests (χ^2_1 = 5.36, $P = 0.02$). Unparasitized nests (unmanipulated: probability of success = 0.51, 95% CI = 0.38, 0.64; cowbird removal: probability of success = 0.63, 95% CI = 0.50, 0.73), had a higher probability of success than parasitized nests (unmanipulated: probability of success = 0.05, 95% CI = 0.03, 0.06; cowbird removal: probability of success = 0.23, 95% CI = 0.18, 0.35). Controlling for parasitism status, the odds of success on cowbird removal plots was 3.1× (95% CI = 1.7, 5.4) greater than the odds of success on unmanipulated plots. Controlling for treatment, the odds of success of an unparasitized nest was 10.6× (95% CI = 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 (χ^2_1 = 7.3, $P = 0.007$) and parasitism status (χ^2_1 = 27.7, $P < 0.001$) explained significant variation in the probability of success. Nests on cowbird removal plots had a higher probability of success (unparasitized: probability of success = 0.67, 95% CI = 0.56, 0.76; parasitized: probability of success = 0.31, 95% CI = 0.21, 0.43), compared to nests on unmanipulated plots (unparasitized: probability of success = 0.48, 95% CI = 0.36, 0.60; parasitized: probability of success = 0.17, 95% CI = 0.11, 0.25). For both treatments combined, unparasitized nests were more likely to fail during the incubation stage than during the brood rearing stage (χ^2_1 = 8.8, $P = 0.002$; $n = 131$).

The number of vireo fledglings per nest was higher on cowbird removal plots (mean = 1.1 ± 0.1 SE) than on unmanipulated plots (mean = 0.4 ± 0.05; $F_{1, 406}$ = 34.7, $P < 0.001$; Fig. 3.3A). Unexpectedly, productivity of cowbird young from vireo nests was also higher on removal plots (mean = 0.1 ± 0.03 young per nest) than on unmanipulated plots (0.06 ± 0.01; $F_{1, 406}$ = 12.8, $P < 0.001$; Fig. 3.3B). We found no evidence of carry-over effects on the mean (± SE) number of vireo fledglings per nest for KP1 (2004 removal year = 1.27 ± 0.33, $n = 26$; 2005 unmanipulated year = 0.12 ± 0.09, $n = 51$), or for KP2 (2004 removal year = 1.03 ± 0.28, $n = 35$; 2005 unmanipulated year = 0.46 ± 0.18, $n = 46$) when compared to the permanent unmanipulated plot (KP5) in 2005 (0.19 ± 0.11, $n = 42$). Thus, vireo productivity per nest returned to pre-removal levels after trapping was suspended.

The number of vireo fledglings produced per vireo egg in unparasitized nests was similar on cowbird removal plots (pooled = 0.57, $n = 228$) and unmanipulated plots (pooled = 0.53, $n = 287$; Table 3.3). 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. Six parasitized nests fledged vireo young; in three the cowbird egg was laid before the vireo nest was complete and was incorporated into the nest lining, in one the cowbird egg failed to hatch, and in two the cowbird egg was laid during vireo incubation and each nest produced one vireo and one cowbird fledgling. Cowbird fledglings per egg was higher on cowbird removal plots (0.15, $n = 95$) compared to unmanipulated plots (0.04, $n = 536$).

Seasonal fecundity and parasitism frequency were highly correlated and parasitism frequency explained 93% of the variation in vireo fledglings per pair ($P = 0.009$). Vireo pairs fledged more vireo young on cowbird removal plots (mean = 2.6 ± 0.2 SE young per pair) compared to unmanipulated plots (1.2 ± 0.1; $F_{1, 118}$ = 22.7, $P < 0.0001$; Fig. 3.3C). Vireo pairs

fledged more cowbird young on removal plots (mean = 0.3 ± 0.06) than on unmanipulated plots

(0.1 ± 0.03; $F_{1, 118}$ = 5.24, $P < 0.02$; Fig. 3.3D).

Effect size estimates

Effect sizes for seasonal fecundity of vireos (2004: $d = 0.78 ± 0.07$ variance; 2005: $d = 0.96 ±$

0.08) and cowbird productivity per vireo pair (2004: $d = 0.59 ± 0.07$; 2005: $d = 0.59 ± 0.07$) were

positive in both years. Cowbird removals increased host productivity of the same magnitude as

of Song Sparrows (1997: $d = 0.74 ± 0.07$; 1998: $d = 1.02 ± 0.08$). In contrast, cowbird removals

decreased cowbird productivity from Song Sparrows (1997: $d = -0.43 ± 0.07$; 1998: $d = -0.36 ±$

0.07). Thus, cowbird removal consistently increased productivity for these songbird hosts, but

our results are opposite in that cowbird removals also increased cowbird productivity.

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. First,

localized cowbird removals had a limited effect on cowbird densities but reduced the probability

of parasitism and the number of cowbird eggs per parasitized nest, and had the desired effect of

increasing vireo productivity per nest and seasonal fecundity. Our results were consistent among

years and replicate plots, and removal of cowbird traps had no obvious carry-over effects on the

probability of parasitism or vireo productivity or fecundity. Cowbird removals resulted in a 10-

fold increase in vireo productivity per nest, but only a 2-fold increase in seasonal fecundity.

Despite the difference in the magnitude of the effect, the trend was consistent with higher

productivity and fecundity on cowbird removal plots. The seasonal decrease in parasitism at our

study site allowed some pairs that deserted previous nests due to cowbird activity or predation to

raise an unparasitized brood, but was not sufficient to increase vireo productivity on

unmanipulated plots to levels similar to those on cowbird removal plots. Second, the probability

of nest desertion was lower on cowbird removal plots relative to unmanipulated plots because

more vireo eggs remained, on average, in parasitized nests. Thus, vireos experienced the cue to

desert less often when cowbird density was experimentally reduced (Chapter 2). 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 on unmanipulated plots than on

cowbird removal plots, possibly due to reduced cowbird density. Last, and counter to our

prediction, cowbird removals had the undesirable effect of increasing cowbird productivity from

vireo nests. Incomplete cowbird removals led to moderate reductions in cowbird densities, but

did not eliminate parasitism. Thus, parasitized nests on removal plots contained more vireo eggs

on average, which in turn reduced the probability of nest desertion (Chapter 2). As a result,

cowbird productivity increased due to a larger number of active parasitized nests and an

increased probability of nest success on the removal plots compared to the unmanipulated plots.

Understanding how parasitism and predation interact to limit host productivity is

essential to successfully managing 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 the primary nest predator

(Smith et al. 2002, 2003). Vireo productivity increased primarily due to decreases in parasitism

because unparasitized nests, regardless of treatment had similar probabilities of nest success and

produced similar number of vireo fledglings per egg. Using seasonal fecundity estimates

(females fledged per female) from this study, an adult survival rate of 0.61 from a Bell's Vireo

population in Missouri (Budnik et al. 2001), and a juvenile survival rate half that of adult

survival (0.30), the finite rate of population growth (λ = female survival rate + (fecundity $\times$ juvenile survival rate)) was 0.79 on unmanipulated plots and 1.0 on cowbird removal plots. Thus, high rates of cowbird parasitism at our study site results in a declining vireo population (λ < 1.0). Further reductions in parasitism at our study site will likely lead to increased vireo productivity and population growth.

The probability of nest success was lower for parasitized nests than unparasitized nests. This pattern should emerge only at high cowbird densities when female laying ranges overlap, and this result supports a key prediction of the cowbird predation hypothesis. At high cowbird densities, nests that escape parasitism during the host laying stage, which is the primary period of cowbird parasitism, should be less likely to be located by cowbirds at later stages. Alternatively, parasitized nests could 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 was not a factor, than failed during the brood rearing stage. Parasitized nests had a higher probability of success on cowbird removal plots than on unmanipulated plots, providing further evidence that cowbirds may depredate parasitized nests at our study site. Understanding patterns of predation for parasitized and unparasitized nests is important because large-bodied hosts (e.g., Dickcissel) can fledge host and parasite young from a single brood, and increased survival of parasitized nests could increase productivity in some host species.

Cowbird productivity from vireo nests was higher on cowbird removal 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 suitable host density (i.e., hosts that can

successfully fledge a cowbird young) is low relative to cowbird density. Although vireos did not

fledge multiple cowbird nestlings from a single nest, cowbird removal could increase cowbird

productivity from host species capable or 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 2005a). Thus,

cowbird populations may be self-limiting in areas with high cowbird densities due to facilitation

of nest desertion, reduced hatching or fledging success due to high rates of multiple parasitism,

or depredation of nests parasitized by other female cowbirds. Our study demonstrates the

importance of understanding the overall effect of cowbird removal on host and cowbird

population dynamics, and community-wide studies are needed to determine if increases in

cowbird productivity are offset by decreases.

The effects of cowbird 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 population size has increased 8-fold.

Although productivity on reference areas was not monitored and the effects of removal on

productivity 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).

Although parasitism frequency was lower on cowbird removal plots, nest failure rates were high

and masked the effect of removals in one study year. Thus, the benefits of cowbird removals can vary regionally for a species and depend on patterns of parasitism and predation.

Small-bodied hosts with long incubation periods typically suffer the highest costs of parasitism (Hauber 2003). However, based on effect size estimates, cowbird removals had a similar effect on productivity for the larger bodied Song Sparrows (20 g) compared to Bell's Vireo (9 g). Increased Song Sparrow productivity resulted from decreased parasitism frequency and increased survival rate of sparrow nests (Smith et al. 2002), whereas Bell's Vireos benefited primarily from decreased parasitism frequency (this study). 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. Although productivity data were not presented, 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 nest failure rates, and host body size may not be a reliable indicator of how the species will respond to experimentally decreased parasitism.

Management implications

The uncertainty of how the termination of cowbird removal programs will affect the productivity and population size of endangered species such as Kirtland's Warbler (*Dendroica kirtlandii*), Black-capped Vireo, and Least Bell's Vireo makes proposals for discontinuation controversial (Rothstein and Peer 2005). We found that after cowbird removals were suspended, parasitism frequency and vireo productivity returned to pre-trapping levels presumably because cowbirds immigrated from surrounding areas. Similarly, Smith et al. (2002) found that parasitism increased and productivity of Song Sparrows decreased following the removal of cowbird traps. If the number of female cowbirds captured at the hosts' breeding area is an indicator of

parasitism potential, then our results indicate that parasitism frequency might return to baseline

levels if long-term trapping is suspended where female cowbird densities or capture rates are

high (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. Additional management interventions such as

reduced livestock density in surrounding areas or habitat restoration may be necessary to ensure

host productivity meets recovery objectives in the absence of trapping (Goguen and Mathews

1999).

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Table 3.1 Logistic regression model results for the probability of parasitism and desertion of parasitized Bell's Vireo nests.

|	AIC_c	ΔAIC_c	K	Deviance	w_i
Probability of parasitism					
Week, Treatment	418.7	0.0	3	412.7	0.56
Year, Week, Treatment	419.5	0.8	4	411.4	0.37
Year, Week, Treatment, Plot	424.1	5.4	8	407.7	0.04
Global	425.7	6.4	9	407.2	0.02
Treatment	443.0	24.3	2	439.0	0
Year, Treatment, Year×Treatment	443.3	24.6	4	435.3	0
Year, Treatment	445.0	26.3	3	439.0	0
Year, Treatment, Plot	448.6	29.9	7	434.4	0
Week	459.1	40.4	2	455.1	0
Probability of nest desertion					
Week, Treatment	335.3	0.0	3	329.2	0.48
Treatment	336.9	1.6	2	332.8	0.22
Year, Week, Treatment	337.3	2.0	4	329.2	0.18
Year, Treatment	338.7	3.4	3	332.6	0.09
Year, Treatment, Year×Treatment	340.7	5.4	4	332.6	0.03
Year, Week, Treatment, Plot	344.7	9.4	8	328.2	0
Year, Treatment, Plot	345.8	10.5	7	331.4	0
Global	346.6	11.3	9	327.9	0
Week	361.0	25.7	2	357.0	0

Notes: ΔAIC_c is the difference between the Akaike Information Criterion value of the best fitting model ($\Delta AIC_c = 0$) and the addition models; K is the number of parameters; w_i is the Akaike weight. The global model is Year, Week, Treatment, Plot, Year×Treatment.

Table 3.2 Productivity estimates (mean ± SE) for Bell's Vireos and Brown-headed Cowbirds from unmanipulated (U) and cowbird removal (R) plots in the Flint Hills region of northeastern Kansas, 2003-2005.

Year	Trt	No. vireo eggs per unparasitized nest (n)	No. vireo eggs per parasitized nest (n)	No. cowbird eggs per parasitized nest (n)	No. vireo fledglings per vireo egg for unparasitized nests (n)	No. vireo fledglings per vireo egg for parasitized nests (n)	No. cowbird fledglings per cowbird egg for parasitized nests (n)
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: Sample size (*n*) for number of eggs per nests is number of nests, and sample size (*n*) for fledglings per egg is number of eggs.

Figure 3.1 Percentage of Bell's Vireo nests parasitized (black bars), multiple parasitism (>1 cowbird egg per parasitized nest, white bars), and deserted (gray bars) on cowbird removal and unmanipulated plots in northeastern Kansas, 2003–2005. Plots are unmanipulated unless labeled 'removal'; sample size is in bar.
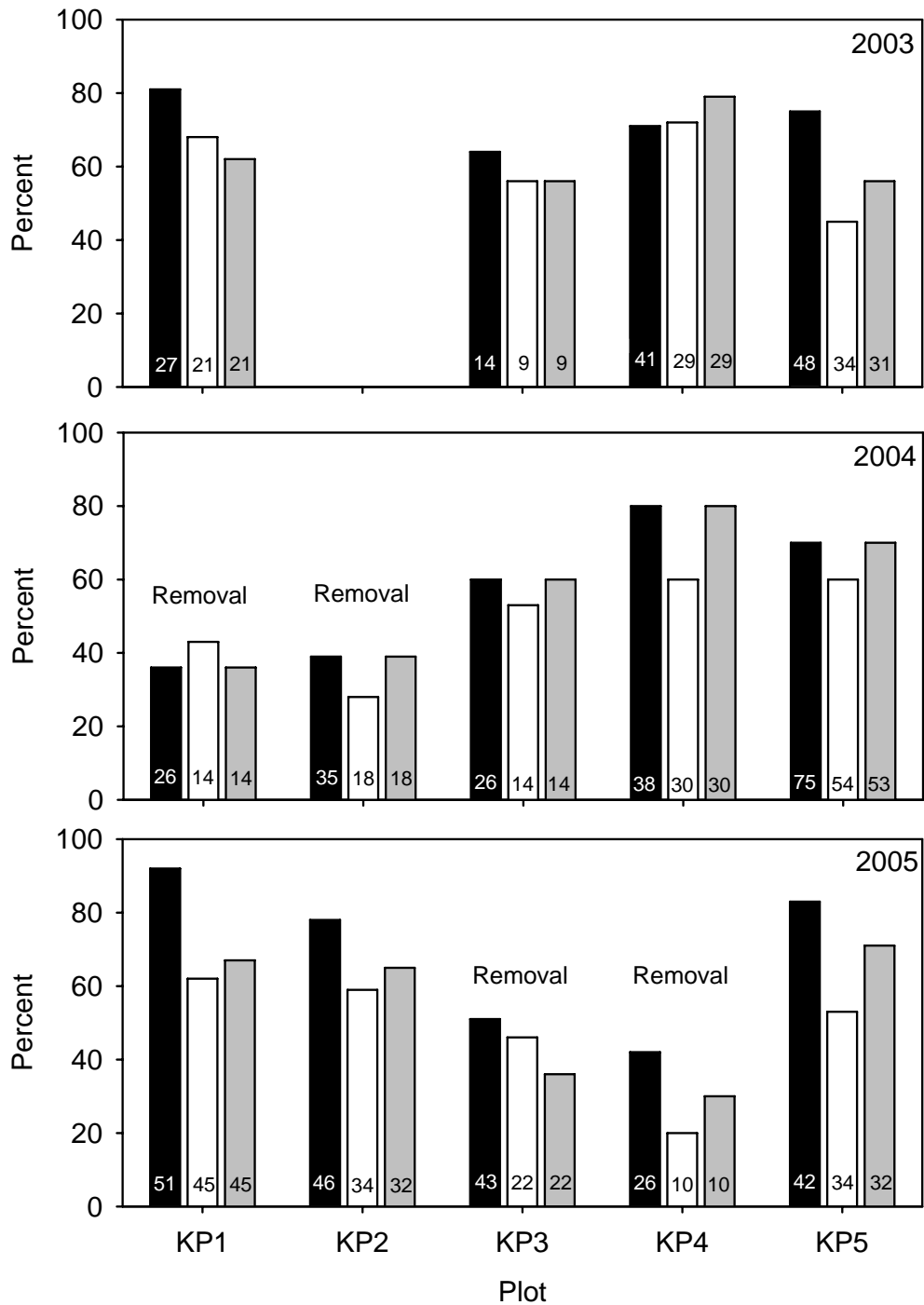
Figure 3.2 (A) Proportion of Bell's Vireo nests parasitized, and (B) proportion of parasitized Bell's Vireo nests deserted by week on unmanipulated and Brown-headed Cowbird removal plots in northeastern Kansas. The logistic regression lines are fit by treatment with years pooled for each analysis. The 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.
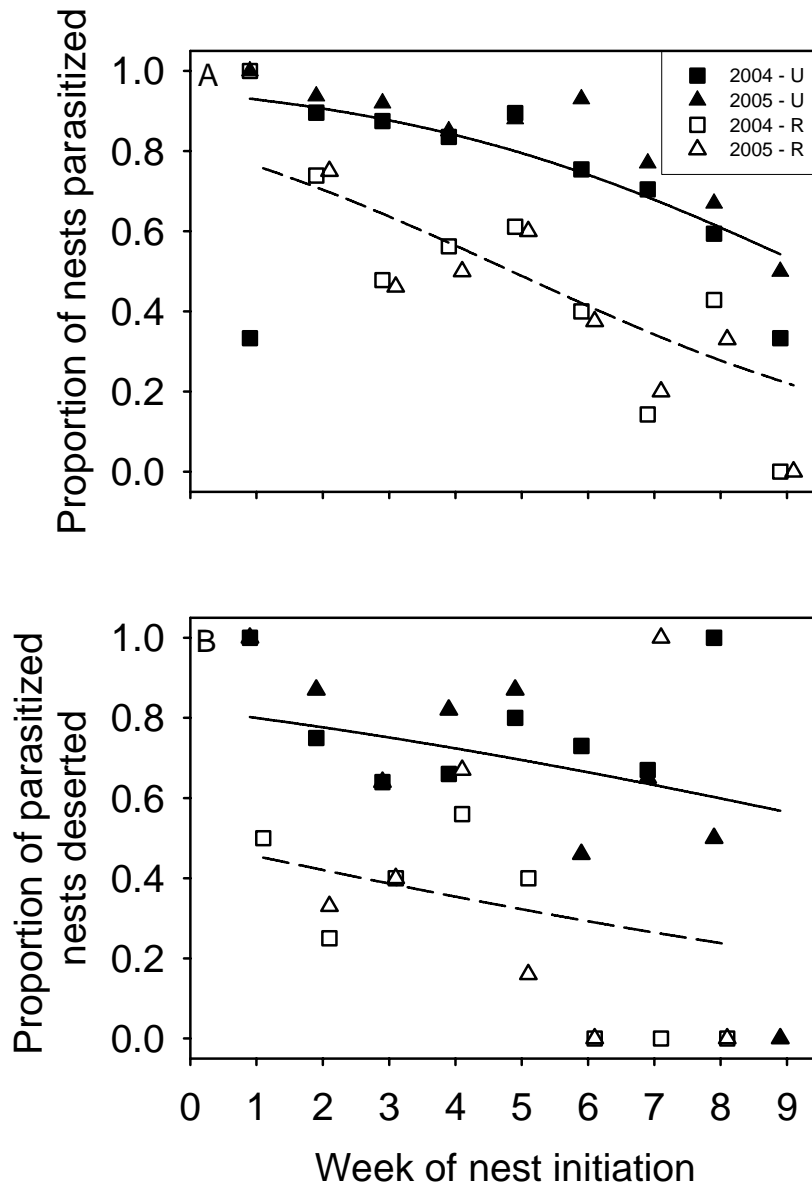
Figure 3.3 (A) Mean (± se) Bell's Vireo fledglings per nest, (B) mean (± se) Brown-headed Cowbird fledglings per Bell's Vireo nest, (C) mean (± se) Bell's Vireo fledglings per vireo pair, and (D) mean (± se) Brown-headed Cowbird fledglings per vireo pair on unmanipulated plots (filled bars) and Brown-headed Cowbird removal plots (open bars) in northeastern Kansas. U = unmanipulated plot, R = cowbird removal plot; results from ANOVA and mixed model: *** = $P < 0.001$, ** = $P < 0.01$, * $P < 0.05$.
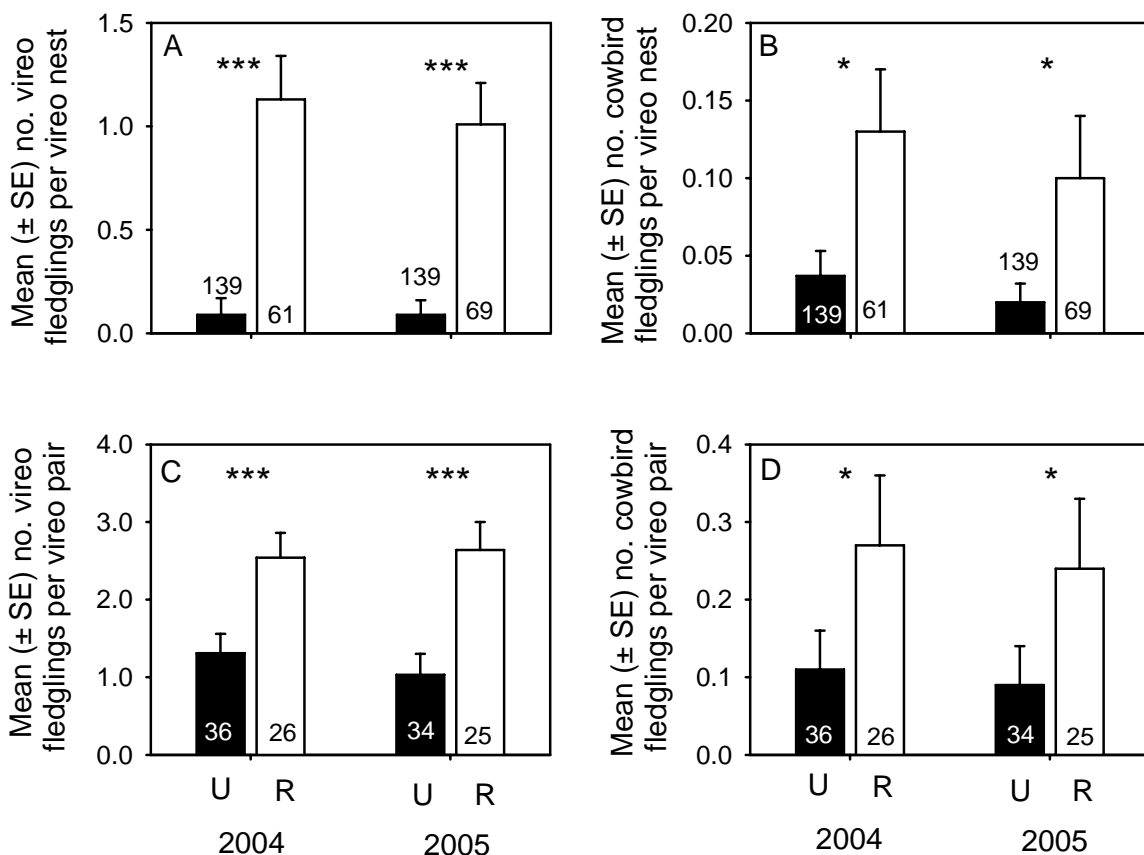
CHAPTER 4 - ASSESSING HABITAT AND HOST USE OF A GENERALIST BROOD PARASITE WITH STABLE ISOTOPE ANALYSIS

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ABSTRACT

Brown-headed Cowbirds (*Molothrus ater*) are generalist brood parasites that parasitize songbird hosts in a wide range of habitats including grasslands and forests. Identifying sources of cowbird fledglings at a landscape scale is challenging because many songbird species produce cowbird young and nest-searching can be time-consuming. Stable isotope analysis of feathers from juveniles may help to identify source habitats of cowbird young because feathers retain the isotopic composition of the diet fed to nestlings by host parents. To assess whether juvenile cowbirds could be linked to habitats or host species, we sampled nestling cowbirds in grassland and shrub habitats and measured carbon (^{13}C) and nitrogen (^{15}N) isotope compositions of feathers. We also sampled feathers from locally fledged juvenile cowbirds and retained underwing coverts from yearling males, which we consider representative of regionally fledged juveniles, to examine changes in post-fledging diet. Feathers from nestlings raised in grassland plots contained more ^{13}C (median = -13.0 ‰, $n = 11$) compared to nestlings reared in shrub plots (median = -21.3‰, $n = 9$). In contrast, feathers from nestlings reared in grassland plots were more depleted in ^{15}N (median = 3.9‰) than feathers from nestlings raised in shrub plots (median = 5.2‰). Of the juveniles sampled, > 70% were classified as originating from shrub plots. Juvenile diets changed post-fledging and were similar to adult diets, suggesting that juveniles

follow foraging behaviors of adults. At both local and regional scales, shrub-encroached habitats appear to be an important source of cowbird fledglings. Continuing expansion of woody plants into tallgrass prairie may be detrimental to grassland birds if it results in increased cowbird productivity.

INTRODUCTION

Identifying host species or habitats in a heterogeneous landscape that serve as major sources of avian brood parasite fledglings is challenging because generalist species such as the Brown-headed Cowbird (*Molothrus ater*; hereafter 'cowbird') parasitize a wide range of songbird species in many different habitats (Rothstein 1975, Woolfenden et al. 2003). Radio-telemetry has been used to identify habitats used by cowbirds for foraging, but has provided limited insights for parasitic behavior because females are difficult to track to host nests (Rothstein et al. 1984, Thompson 1994, Goguen and Mathews 2001). Moreover, individual females will parasitize multiple host species within a community (Gibbs et al. 1997, Alderson et al. 1999, Woolfenden et al. 2003). Community-wide patterns of host use are challenging to obtain, and most studies report parasitism frequencies for a subset of host species and at limited spatial scales (Dececco et al. 2000). Furthermore, population estimates of cowbird productivity would require data from all host species in a study area, but the challenge of locating all parasitized nests has limited demographic profiles of cowbird productivity to habitats or single host species (Winter 1999, Davis 2003, Johnson and van Riper 2004, Woolfenden et al. 2004).

Understanding habitat- and host-specific patterns of cowbird productivity is critical because cowbirds often reduce the nesting success and population growth of songbird hosts (Robinson et al. 1995, Rogers et al. 1997, Ward and Smith 2000). Cowbird control is a component of recovery plans for endangered songbirds throughout the US, and management interventions

range from removing or addling cowbird eggs to lethal control of adults (Rothstein and Peer

2005). While parasitism frequency and cowbird productivity are intensively studied for

endangered songbirds, the productivity of cowbirds from other hosts in the community is poorly

understood (DeCapita 2000, Kostecke et al. 2005, Kus and Whitfield 2005). Ultimately,

identifying the habitats that produce a majority of juvenile cowbirds would allow managers to set

priorities and also improve upon parameters essential for demographic and population growth

models for cowbirds.

The use of stable isotopes in animal ecology has helped to elucidate migratory

connectivity, breeding origins, and diet of birds (West et al. 2006). Hydrogen isotope (^{2}H or

deuterium) analysis has enabled researches to estimate breeding latitude of birds captured on the

wintering grounds because feathers grown on the breeding grounds retain isotopic information

from that area (Hobson and Wassenaar 1997, Kelly et al. 2005). Carbon isotope (^{13}C) analysis

can be used to determine habitat use during the time of tissue growth because C_3 plants (e.g.,

trees, shrubs, forbs) and C_4 plants (e.g., native warm season grasses) have different

photosynthetic pathways that create distinct isotopic compositions (Farquhar et al. 1989).

Nitrogen isotope (^{15}N) analysis can be used to investigate trophic level of the species because the

δ^{15}N composition is typically enriched 3–5 ‰ with each trophic level (Hobson and Clark 1992,

Romanek et al. 2000). Stable isotope analysis of feathers may be an additional technique that

can help identify habitats or host species that serve as sources of cowbird fledglings. Feathers

grown by nestlings should reflect the isotopic composition of the diet fed by the host parents

(Duxbury et al. 2003) because feathers are structurally inert once growth is complete and retain

the isotopic composition until molted and replaced. In addition, stable isotope analysis can be

used to examine changes in diet and habitat use of fledglings that otherwise could only be accomplished by gut content analysis or by following marked individuals.

Here, we used stable isotope analysis to investigate habitat- and host-specific patterns of cowbird productivity and to examine post-fledging changes in diet. We assessed the variation in carbon and nitrogen isotopic ratios of cowbird nestlings from songbird hosts nesting in prairie plots dominate by of native warm season grasses (C_4 species) and in shrub plots heavily encroached by woody shrubs and forbs (C_3 species). We compared isotopic ratios among nestlings, juveniles, and yearlings to determine if cowbird production could be linked to habitat or host species. In prairie fragments, parasitism frequencies tend to be higher near wooded edges or in shrub-encroached areas, and these patterns may be influenced by the availability of elevated perches that provide female cowbirds with a vantage point to observe host nesting activity (Strausberger and Ashley 1997, Robinson et al. 1999, Winter et al. 2000, Jensen and Finck 2004, Patten et al. 2006). Thus, we hypothesized that shrub plots serve as a major source of cowbird fledglings and predicted that the feather isotopic ratios of juvenile cowbirds should be consistent with the composition of nestlings raised in the shrub plots. At independence, juvenile cowbirds join foraging flocks of adults, but it is unknown if juveniles follow foraging patterns of adults. We hypothesized that the nestling diet does not influence the post-fledging diet of juvenile cowbirds, and predicted that yearlings would not differ isotopically from adults because juveniles associate with adults after fledging from hosts nests.

METHODS

Study site and host community

In 2005, feathers were collected from cowbirds breeding at the Konza Prairie Biological Station (39º05' N, 96º35' W) in northeastern Kansas. Konza Prairie is part of the tallgrass prairie

ecosystem, which has been reduced to a core area in the Flint Hills region of Kansas due to row-crop agriculture. Most of the Flint Hills is managed for cattle production and is burned annually, and the vegetation is dominated by native warm season grasses (C_4 species). Konza Prairie is a 3,267 ha long-term ecological research site, that is partitioned into about 60 experimental plots that are experimentally manipulated with different combinations of fire and grazing treatments. Fire frequencies range from annual to every 20 years and grazing treatments include bison, cattle, and no grazing (Hartnett et al. 1996). In plots with regular fire intervals of one to three years, the dominant vegetation is warm season grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), and switch grass (*Panicum vigratum*). In plots with fire suppression and fire intervals > three years, woody shrubs become more abundant and include rough-leaved dogwood (*Cornus drummondii*), American plum (*Prunus americana*) and smooth sumac (*Rhus glabra*; Briggs et al. 2005). Based on the fire frequency and plant community we refer to annually-burned grass dominant plots as 'grassland plots' and shrub-encroached plots burned at intervals greater than three years as 'shrub plots'.

The avian community of Konza Prairie is comprised of grassland, shrubland, and forest breeding species (Zimmerman 1993). Based on line transect surveys, Dickcissels (*Spiza americana*) are the most abundant cowbird host nesting at Konza (mean = 12.8 individuals/km), and other common grassland hosts such as Eastern Meadowlarks (*Sturnella magna*; 6.4 individuals/km) and Grasshopper Sparrows (*Ammodramus savannarum*; mean = 5.3 individuals/km) occur at lower abundances (Powell 2006). Although these species are considered 'grassland birds', they breed in shrub-encroached plots with fire frequencies > three years (Powell 2006). Common shrub-nesting hosts that accept cowbird eggs include Bell's

Vireo (*Vireo bellii*), and Field Sparrow (*Spizella pusilla*). While most grassland hosts accept cowbird eggs, egg ejection is more common in shrub-nesting and forest-nesting hosts, and common rejecter species on Konza Prairie include Gray Catbird (*Dumetella carolinensis*) and Brown Thrasher (*Toxostoma rufum,* Peer and Sealy 2004). In the northern Flint Hills, > 70% of grassland bird nests receive at least one cowbird egg, and multiple parasitism is common (Elliott 1978, Jensen and Cully 2005). Host productivity of cowbirds varies among species, large-bodied host species such as Dickcissel can raise mixed broods, while small-bodied host species such as Bell's Vireo (*Vireo bellii*) fail to produce host young if successfully parasitized (Parker 1999, Jensen and Cully 2005).

Sampling locations

As part of a larger study on the effects of cowbird removal on shrub-nesting birds, adult cowbirds were sampled from three cowbird traps placed around the perimeter of two shrub plots (Chapter 3). Juveniles were sampled from two traps placed on the boundary between a prairie plot and a shrub plot. Cowbird nestlings were sampled from hosts nests located in plots burned annually and plots burned at intervals greater than three years.

Feather samples

Cowbirds have a molt cycle typical of North American blackbirds and undergo one prebasic molt of body and flight feathers prior to fall migration (Pyle 1997). After fledging from host nests, juvenile cowbirds molt all body and flight feathers except the underwing coverts prior to migration from the natal site. Subsequent molts take place before fall migration on the breeding grounds. Male cowbirds can be aged as yearlings (i.e., second year birds) or adults (i.e., after second year birds) by presence or lack of retained juvenile feathers among the underwing coverts (Ortega et al. 1996, Pyle 1997).

To develop an isotopic profile of host species, we sampled feathers from cowbird nestlings in the nests of known host species located in grassland plots or shrub plots. We collected feather samples from only one cowbird nestling if multiple cowbirds were present. We sampled outer primaries from independent juveniles captured on Konza Prairie between 30 June and 14 July. The host species was unknown, but these juveniles were locally produced because wing feather development was incomplete and flight efficiency was poor. Natal dispersal distances are greater than breeding dispersal distances for many passerine songbirds (Woodworth et al. 1998, Winkler et al. 2005), including cowbirds (Anderson et al. 2005). To examine the isotopic ratios of regionally fledged juveniles and changes in diet post-fledging, we sampled retained juvenile underwing coverts and outer primary feathers from yearling males. Yearling males presumably had completed natal dispersal and may have immigrated to our study site from a larger region. Retained underwing coverts from yearling males have the isotopic composition of the diet fed by hosts, but the flight feathers have the isotopic composition of the food gathered from the natal grounds in the same year. To ensure that only local yearlings and adults were included, all feather samples were obtained from randomly selected cowbirds captured between 1–30 June during the peak of the cowbird breeding season in Kansas (Chapter 3).

Stable isotope analysis

Feathers were cleaned to remove dirt and oil from handling by rinsing with a 2:1 chloroform:methanol solution and allowed to air dry for 48 hours. Approximately 2 mm of the distal portion of feather was removed by clipping and cut into small pieces. Between 1.0 and 1.5 mg of the feather was loaded into tin capsules for carbon and nitrogen isotope analysis. Samples were analyzed with a continuous-flow Thermo Finnigan Delta Plus Mass Spectrometer coupled to a Carlo Erba elemental analyzer (EA 1110). Isotopic composition (R) is expressed as a ratio

of the heavy isotope divided by the light isotope, (e.g., $R = {}^{13}C / {}^{12}C$). This difference can be

small and must be compared to a standard. This change is referred to as delta (δ), and is

expressed in parts per thousand with the following equation:

$$\delta = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000$$

The international standard for carbon (C) is the Pee Dee Belemnite (PDB) limestone formation

and the standard for nitrogen (N) is atmospheric nitrogen. To determine relative contribution (p)

of C_4 plants to the diet, we used a two end-point mixing model (Fleming 1995):

$$\delta^{13}C_{\text{feather}} = p\ (\delta^{13}Cc_{4\text{-plants}}) + (1 - p)\ (\delta^{13}Cc_{3\text{-plants}}) + \Delta$$

where Δ is the diet-tissue fractionation factor (2.0 ‰) between diet and feather for carbon

(Hobson and Clark 1992).

Analytical error

Internal standards were analyzed after every nine unknown samples to monitor drift in isotopic

measurements. While isotopic and elemental drift are not unusual through the course of a run on

a mass spectrometer (>8 hours), the instrument used for this analysis experienced little drift. An

oak leaves standard ($n = 17$) had a mean $\delta^{15}N$ value of -2.8‰ (SD = 0.03‰), and a mean $\delta^{13}C$

value of -28.6‰ (SD = 0.00‰) during runs of our samples. No adjustments were necessary.

Statistical analysis

Stable isotope data are often non-normally distributed and contain outliers. Therefore,

we used the non-parametric Mann-Whitney U and Kruskal-Wallis tests (PROC NPAR1WAY in

SAS) to determine if carbon and nitrogen isotope ratios differed among habitats or age-groups.

If values differed among groups, we conducted multiple comparisons in PROC MULTTEST,

and determined significance using the permutation P-value. To determine if juveniles could be

could be classified to a habitat type; we used discriminant function analysis. We derived the

discriminant function using only data from nestlings from known nests in grassland and shrub

plots and then classified juveniles of unknown sources. We used the leave-one-out method (or

'cross-validation') to determine the proportion of correct classifications. Because retained

underwing coverts and primaries were obtained from the same yearling males and were not

independent, we used a Wilcoxon Signed-Rank test to determine if $\delta^{13}C$ and $\delta^{15}N$ values

changed after fledging.

RESULTS

In grassland plots, we obtained cowbird nestling feathers from 11 nests: Dickcissel ($n = 3$),

Eastern Meadowlark ($n = 2$), Grasshopper Sparrow ($n = 1$), and Red-winged Blackbird (*Agelaius*

phoeniceus, $n = 5$). In shrub plots, we obtained cowbird nestling feathers from 9 nests:

Dickcissel ($n = 6$), Eastern Meadowlark ($n = 2$), and Eastern Towhee (*Pipilo erythrophthalmus*, n

$= 1$). Carbon and nitrogen isotope feather ratios differed between nestlings raised in grassland

plots and shrub plots. Feathers from nestlings raised in grassland plots contained more ^{13}C

(median = -13.0 ‰, $n = 11$) compared to nestlings reared in shrub plots (median = -21.3‰, $n =$

9; $U = 4.0$, $P < 0.001$; Fig. 4.1a). In contrast, feathers from nestlings reared in grass plots were

more depleted in ^{15}N (median = 3.9‰, $n = 11$) than feathers from nestlings raised in shrub plots

(median = 5.2‰, $n = 9$; $U = 79.5$, $P = 0.03$; Fig. 4.1b). Thus, the isotopic ratio of the feathers

co-varied with the habitat from which the nestlings were sampled.

   We had adequate data to compare intraspecific variation by habitat for two hosts.

Cowbirds raised in Dickcissel nests differed isotopically between habitat types, with nestlings

raised in grassland plots being more depleted in both ^{13}C and ^{15}N ($\delta^{13}C$ median = -13.0‰; $\delta^{15}N$

$= 2.9$, $n = 3$) than birds raised in shrub plots ($\delta^{13}C$ median = -22.3‰; $\delta^{15}N$ median = 5.1, $n = 6$).

Cowbird nestlings raised in Eastern Meadowlark nests showed no difference in $\delta^{13}C$ (grass plot

median = -12.4‰, n = 2; shrub plot median = -15.9‰, n = 2) values or δ^{15}N values (grass plot

median = -5.5‰, n = 2; shrub plot median = 6.0‰, n = 2) between habitat types. Red-winged

Blackbirds from grassland plots showed similar isotopic profiles (δ^{13}C median = -14.8‰; δ^{15}N =

3.9, n = 5) as Dickcissel from grassland plots (δ^{13}C median = -13.0‰; δ^{15}N = 2.9, n = 3).

Carbon isotope values differed among locally fledged juveniles, regionally fledged

juveniles, and nestlings sampled on Konza Prairie (Kruskal-Wallis test, χ^2_3 = 25.0, P < 0.001).

Local juveniles (δ^{13}C median = -21.1‰) and regional juveniles (δ^{13}C median = -18.3‰) differed

(P = 0.05), and both types of juveniles were more depleted in ^{13}C than nestlings from grassland

plots (local and regional: P < 0.001). Delta ^{13}C values from local or regional juveniles did not

differ from nestlings raised in shrub plots (local: P = 0.98; regional: P = 0.20). Nitrogen isotope

values did not differ among groups (Kruskal-Wallis test, χ^2_3 = 7.6, P = 0.06).

The discriminant function analysis provided sufficient resolution to separate nestlings

into grassland and shrub habitat based on δ^{13}C and δ^{15}N values (χ^2_2 = 22.0, P < 0.0001; Fig. 4.2).

Using the leave-one-out method, 90% of the nestlings were correctly classified; all of the

nestlings from grass plots were classified correctly (n = 11), and 78% of nestlings from shrub

plots were classified correctly (n = 9). Eighty-seven percent of locally produced juveniles (n =

15) and 73% of the regionally produced juveniles (n = 15) were classified with nestlings from

shrub plots.

Retained juvenile underwing coverts from yearlings were more depleted in ^{13}C than the

primaries grown during the first pre-basic molt (Wilcoxon Signed-Rank test S = -60.0, P <

0.001; Fig. 4.1a). Mean contribution of C_3-based food items was high in nestling diets (64% ±

18% SD), but decreased post-fledging (mean = 24% ± 10% SD), and all individuals increased

consumption of C_4-based foods. Primaries grown during the first pre-basic molt contained more

^{15}N than retained juvenile underwing coverts (Wilcoxon Signed-Rank test: $S = -44.50$, $p = 0.008$; Fig. 4.1b). Carbon ($U = 109.0$, $p = 0.68$) and nitrogen ($U = 87.0$, $p = 0.20$) isotope values from yearling male primaries grown during the first pre-basic molt did not differ from adult male primaries grown post-breeding.

DISCUSSION

The major results of this study demonstrate that stable isotopes can provide insights into habitat-specific productivity by the brood parasitic Brown-headed Cowbird. The isotopic composition of cowbird nestlings co-varied with natal habitat; nestlings raised in grass plots contained more ^{13}C and were more depleted in ^{15}N than nestlings raised in shrub plots. Based on discriminant function analysis, 90% of the nestlings were correctly classified to the habitat from which they were sampled. We found that locally fledged juveniles did not differ isotopically from nestlings raised in shrub plots, suggesting higher cowbird productivity from shrub-encroached habitats in tallgrass prairie. Isotope ratios from Red-winged Blackbirds and Dickcissels from grassland plots were similar. Thus, assigning juveniles to host species may be challenging due to overlap in isotope profiles for some species. The contribution of C_4-feeding insects to the juvenile diet increased post-fledging among yearling males, and carbon and nitrogen values did not differ from adult males suggesting that juveniles follow foraging patterns similar to adults.

Our analysis suggests that shrub habitats in tallgrass prairie are important sources of cowbird fledglings because carbon isotope values from fledglings were identical to nestlings raised in this habitat, and >70% of all juveniles were classified with nestlings from shrub plots. Furthermore, nestlings from grassland plots showed little contribution of C_3-feeding insects to the nestling diet. The pattern of cowbird productivity that emerged from our isotope analysis is supported by studies that found higher parasitism frequencies near wooded edges in prairie

fragments and on heterogeneous landscapes (Strausberger and Ashley 1997, Robinson et al. 1999, Winter et al. 2000, Jensen and Finck 2004). Although we did not sample cowbird nestlings from forest-nesting host species, it is unlikely that these hosts fledged the majority of juveniles we sampled because the carbon isotope ratios of nestlings from forests would be similar to C_3 plants (-24‰) when adjusted for fractionation (e.g., Hobson 1999, Hobson et al. 2004).

We found isotopic evidence for a post-fledging shift in the nestling to juvenile diet cowbirds but no indication of age-specific diets among older age-classes of males. Our individual-based analysis revealed that feathers grown during the nestling period showed a substantial contribution of C_3-feeding insects to the diet, whereas feathers grown during the first prebasic molt showed a strong contribution of C_4-feeding insects to the diet. In addition, higher $\delta^{15}N$ values for yearlings indicate that individuals fed at a higher trophic level post-fledging relative to the nestling diet. Our results suggest that regardless of natal habitat, juveniles recruit into adult flocks and feed in grass dominated habitat prior to fall migration, and follow similar foraging patterns as adults. Stable isotope analysis has been used to identify age-specific diets for a number of bird species, and juveniles often isotopically differ from adults where trophic partitioning is observed (Hodum and Hobson 2000, Forero et al. 2002). However, these studies used different individuals from each age class, and no previous study has used feathers from known-aged birds to examine individual changes in diet.

Stable isotope analysis of nestling generalist brood parasites is a novel approach for the study of habitat-specific cowbird productivity. We established an isotopic profile of the natal habitats from carbon and nitrogen values obtained from nestling feathers and not from plant tissue or soil samples, as in some other isotope studies (e.g., Evans Ogden et al. 2005). Thus, the

values obtained from nestlings represent the integration of the resources used by host species for the nestling diet. A similar method was used to assign American Redstarts (*Setophaga ruticilla*) to winter habitats because wintering birds establish territories in mangroves and second-growth shrub habitat and show habitat-specific isotope compositions (Marra et al. 1998, Hobson 1999). Our analysis of nestling feathers demonstrates that in a heterogeneous tallgrass prairie habitat, host species may create habitat-specific isotopic profiles for cowbird nestlings, which enabled us to match juveniles of unknown origin to source habitats. This approach could be extended to other birds where a sufficient number of nestlings could be sampled in order to develop the isotopic profile of natal areas, and individuals captured at a later date can be assigned back to natal areas (Romanek et al. 2000).

Due to the limitations of large-scale nest monitoring projects to estimate habitat- and host-specific cowbird productivity, indirect methods that utilize information carried by fledglings, such as stable isotopes or lice are of increasing value. Many species of avian lice (Phithiraptera) are host-specific (Hopkins 1942, Tompkins and Clayton 1999), and recently fledged cowbird young may carry lice transferred from the nest mates or foster parents, thus enabling investigators to identify the host species (Hahn et al. 2000, Hahn and Price 2001). However, two complications exist in practice, some juveniles may not carry lice and the most prevalent lice species may be found on multiple host species (Hahn et al. 2000, Clayton and Johnson 2001, Clayton and Johnson 2001). Thus, stable isotope analysis may represent a more general but complimentary method of identifying source habitats or host species that produced juvenile cowbirds.

Shrub expansion into mesic grasslands of North America creates habitats that are favorable for foraging and reproduction by cowbirds. Broad scale fire suppression has facilitated

the establishment of woody plants, and mechanical removal may be necessary to restore

grasslands to historic plant communities (Briggs et al. 2002, Briggs et al. 2005). In addition,

shrub-encroachment may reduce the breeding habitat of grassland birds, a declining group in

North America (Grant et al. 2004, Van Dyke et al. 2004, Brennan and Kuvlesky 2005). Shrub-

encroached pastures, such as those present on Konza Prairie, are beneficial for cowbirds because

movements between breeding and foraging areas may be greatly reduced if livestock forage near

shrubs. Long daily commuting distances (> 5 km) between foraging and breeding areas are

thought to reduce cowbird productivity because of energy and time expended on daily

movements (Rothstein et al. 1984, Goguen and Mathews 2001). Cowbird fledglings may also

benefit from woody expansion because nestlings raised in shrub-encroached habitats may have

greater success locating adult flocks foraging with livestock in nearby grasslands. Thus, shrub

expansion into grassland habitats may be deleterious for grassland birds not only because it

reduces habitat, but it may increase risk of parasitism because of greater productivity of cowbirds

from shrub-nesting birds in habitats with woody encroachment.

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Figure 4.1 Box and whisker plots for (a) δ^{13}C values, and (b) δ^{15}N values obtained from Brown-headed Cowbird feathers sampled in Kansas. Nestling cowbirds were reared in host nests in grass plots or shrub plots. Juveniles were trapped on Konza Prairie in June and July. Yearlings were trapped on Konza Prairie in June; covert feathers from yearlings represent the nestling diet, primary feathers represent the diet of independent juveniles. Adults were captured on Konza Prairie in June. The line in the box is the median and the box is the 25th and 75th percentiles. Whiskers extend to a value within 1.5 times the interquartile range, outliers, values more than 3 times the interquartile range, are indicated by a filled circle. The number above the x-axis is the sample size for carbon and nitrogen.
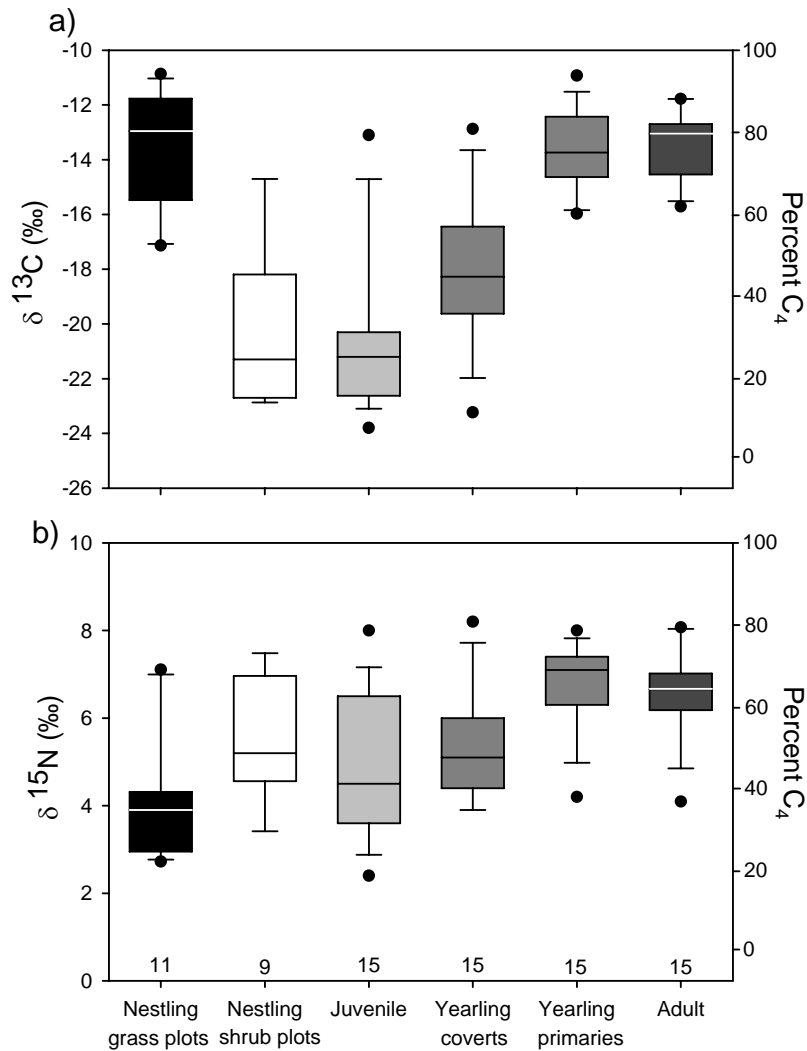
Figure 4.2 Mean (± SD) carbon and nitrogen isotope values from feathers from nestling, juvenile, and yearling cowbirds. Values for locally produced juveniles are from feathers from juveniles captured on Konza Prairie. Values for regionally produced juveniles are from retained juvenile underwing coverts from yearling males trapped on Konza Prairie. Eighty-seven percent of locally produced juveniles and 73% of regionally produced juveniles were classified with nestlings from shrub plots, based on a discriminant function analysis.

● Nestlings - grassland plots (*n* = 11)
□ Nestlings - shrub plots (*n* = 9)
△ Locally produced juveniles (*n* = 15)
◆ Regionally produced juveniles (*n* = 15)
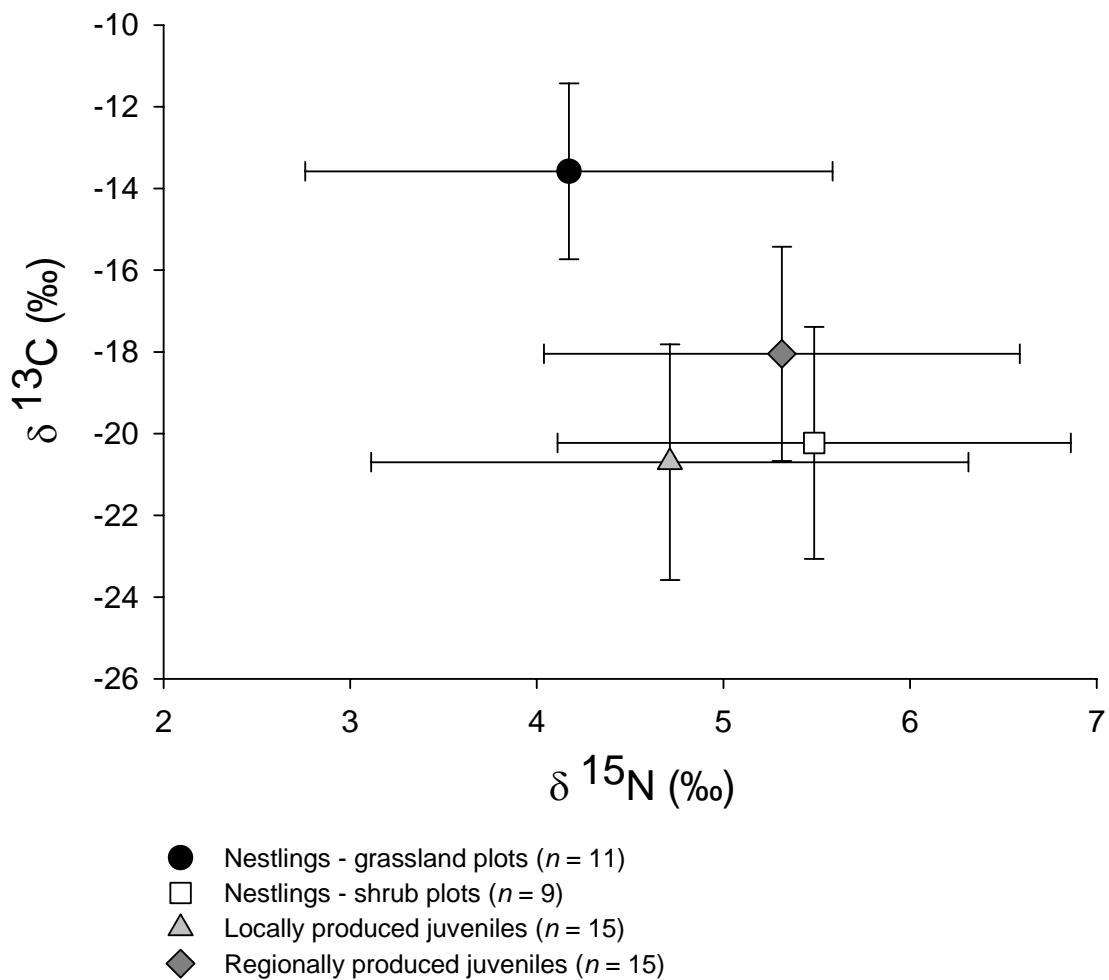
CHAPTER 5 - CONCLUSIONS

Cowbird parasitism can reduce population growth and productivity of host species, and thousands of cowbirds are removed annually as part of management programs for endangered songbirds. Thus, a complete understanding of host defense behaviors, the effects of parasitism on host productivity, and areas of cowbird productivity are necessary for the successful management of host species. In addition, an understanding of these processes would provide valuable empirical support for theoretical predictions of host-parasite co-evolution. The objectives of this research were to 1) identify the cue(s) that causes nest desertion in Bell's Vireos, 2) examine how cowbird removals affect vireo and cowbird productivity, and 3) evaluate the utility of stable isotope analysis in determining natal habitats or hosts of juvenile cowbird. Nest desertion by Bell's Vireos is a generalized response to egg loss. Vireos did not desert nests when cowbird eggs were immediately exchanged for vireo eggs, but deserted when cowbird eggs were exchanged after at least a 12 hour delay. In addition, most vireo pairs accepted and deserted parasitized nests within a season, and response was influenced by the number of host eggs that remained in the nest. Thus, variability in pair response was due to variability in egg loss during each nesting attempt. In conclusion, cues that cause nest desertion should be identified prior to altering management plans of endangered species in order to facilitate the evolution of behaviors that may not be specific anti-parasite behaviors.

Host and parasite productivity increased on cowbird removal plots. Vireo productivity per pair increased substantially on cowbird removal plots because fewer nests were parasitized. Cowbird removals did not increase nest survival, and cowbird parasitism is the primary factor limiting vireo productivity at my study site. Unexpectedly, cowbird removal increased cowbird

productivity from vireo nests because fewer parasitized nests were deserted. This study demonstrates the importance of understanding the overall effect of cowbird removal on host and cowbird population dynamics, and community-wide studies are needed to determine if increases in cowbird productivity are offset by decreases.

Stable isotope analysis may be a valuable tool for identifying habitats that produce cowbird fledglings on the landscape. I found that carbon and nitrogen isotope compositions from nestling cowbirds differed between prairie plots and shrub plots, and >70% of locally produced and regionally produced cowbird juveniles were classified with nestlings from shrub plots. Parasitism frequencies are higher near wooded edges, and continued woody plant encroachment into mesic grasslands may lead to increased cowbird productivity.

In summary, it is difficult to make generalizations about host response to parasitism, the effects of parasitism on host productivity, and areas of cowbird productivity because cowbirds are generalists that will parasitize hosts with varying life history traits across a range of habitats. Moreover, region or site specific processes, such as nest predation can have profound impacts on host productivity and may limit the efficacy of cowbird removals in increasing host productivity. Thus, caution should be used when management recommendations for endangered species are based on results from unrelated hosts breeding in other geographic regions.