

Nest desertion by a cowbird host: an antiparasite behavior or a response to egg loss?

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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 (antiparasite 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. *Key words:* Bell's vireo, brown-headed cowbird, egg predation, evolutionary lag, host–parasite coevolution, *Molothrus ater*, *Vireo bellii*. [*Behav Ecol* 17:917–924 (2006)]

The reproductive strategies of avian brood parasites and the behavioral responses of their hosts have served as a model of coevolution 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 coevolved antiparasite behaviors to reduce fitness costs. Egg ejection is well documented in many hosts that have long coevolutionary histories with cuckoos, and some species eject greater than 80% of nonmimetic eggs (Davies and Brooke 1998). Egg discrimination is not as well developed in cowbird hosts; only 24 of 220 host species regularly reject nonmimetic 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). Although 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).

Although ejection of undamaged parasitic eggs may be a coevolved 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 antiparasite 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

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Received 31 March 2006; revised 24 May 2006; accepted 19 June 2006.

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 (*Vireo bellii 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 3 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 2 sets of hypotheses regarding nest desertion in Bell's vireos. First, we sought to identify the cues that induce desertion. According to the "antiparasite response hypothesis," nest desertion is a specific antiparasite 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 antiparasite 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 1). The antiparasite 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).

METHODS

Field methods

We studied Bell's vireos breeding at Konza Prairie Biological Station in northeastern Kansas, USA (39°05'N, 96°35'W)

Table 1

Predicted behavior of Bell's vireo if nest desertion is due to an antiparasite response or a generalized response to egg predation

Vireo behavior	Behavior consistent with	
	Antiparasite 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-h delay	Yes	Yes

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 drummondii*). 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 2 days after the nest is completed, and modal clutch size of unparasitized vireo nests is 4 eggs. Vireo pairs in our study area frequently reneest after predation or nest desertion but produce one brood per year (KL Kosciuch, unpublished data). To quantify components of reproductive output, we monitored vireo territories and nests every 3 days to determine the 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 10–30% 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

Table 2

Predicted behavior of Bell's vireo if variation in nest desertion response is due to intrinsic (genetic or learned) variation among individuals 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 reneesting attempt after deserting a parasitized nest	No	Yes
Larger change in cue (host or cowbird eggs) intensity more likely to cause desertion	No	Yes

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 3 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 3 days. Only 2% 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, 3 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 intrapair responses to parasitism

To examine intrapair responses to parasitism within a season, we placed pairs that had 2 or more nests parasitized within a season into 3 categories based on response. “Acceptor 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 AM CST on the day the third vireo egg was laid to mimic the time of day when female cowbirds remove host eggs (Sealy 1992; KL Kosciuch, personal observation). We used 2 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; KL Kosciuch, unpublished 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 3 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 the “control” treatment, we removed 2 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 2 vireo eggs and immediately replaced them with 2 cowbird eggs. In “removal” nests, we removed 2 vireo eggs and replaced them with 2 cowbird eggs the next morning before 07:30 AM 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 3 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 3 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):

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

where Dev is the model deviance ($-2 \ln L$), 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 ≤ 2 were considered equally parsimonious. If 2 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 were 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 acceptor pairs, deserter pairs, and mixed-strategy pairs. Nests from mixed-strategy pairs were subdivided into accepted nests and deserted nests. We included pair as a random effect to account for the nonindependence 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 groups 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 \pm SE and statistical tests were 2-tailed with an $\alpha = 0.05$.

RESULTS

Nest desertion in unmanipulated nests

The proportion of nests that were deserted increased as 2 or fewer vireo eggs remained in the nest (Figure 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 3 or 4 vireo eggs ($n = 243$) were not deserted even if 3 or more cowbird eggs were added. When 2 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 2 factors:

the number of vireo eggs remaining and number of cowbird eggs received (Table 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 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 ($w_i = 0.21, \Delta AIC_c = 2.2$).

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:

$$\text{Logit}(P) = 4.51 - 2.47(\text{vireo eggs remaining}) + 0.34(\text{cowbird eggs received}).$$

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 \times (95% confidence interval [CI] = 6.52, 18.36). 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 \times , 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 4). Vireos deserted 100% of the nests when cowbirds removed all 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 4). Vireos did not desert nests

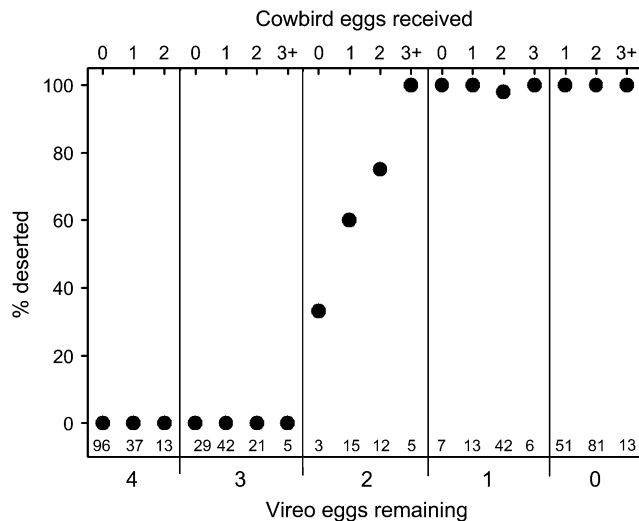


Figure 1 Percentage of nests deserted in relation to natural variation in the number of vireo eggs remaining and cowbird eggs received. Sample size of nests for each combination of vireo and cowbird eggs at the end of laying are listed above the x axis.

Table 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)

Model 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	2.2	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 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 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 laying

Timing of vireo egg removal ^a	% Total clutch removed	% Vireo clutch removed	Nr. of nests	Nr. 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.

when cowbirds removed an egg within 2 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 25–50% 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 2 of 3 vireo eggs were immediately exchanged for cowbird eggs ($n = 7$). However, 83% of removal nests were deserted when 2 of 3 vireo eggs were removed the night before the cowbird eggs were added ($n = 6$). The pair that did not desert the experimental removal nest was attempting its third nest late in the season, and the benefit of remaining with a reduced clutch may have been greater than the benefit of deserting. 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 intrapair responses to parasitism

Of monitored vireo pairs ($n = 88$), 11% were consistently acceptor 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 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 acceptor pairs did not differ from the number of cowbird eggs in the nests of deserter

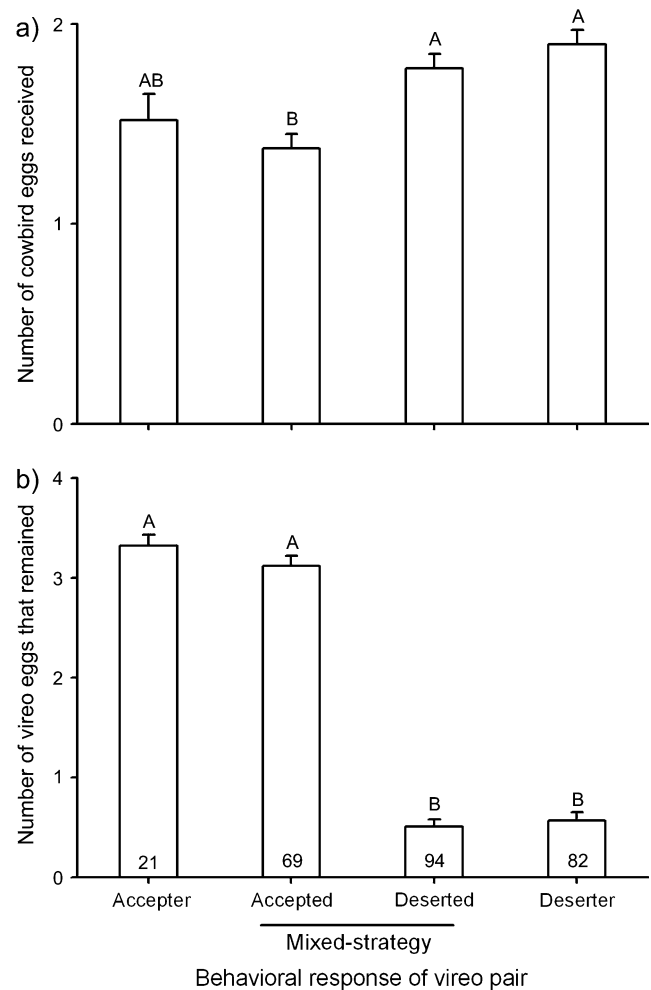


Figure 2
 Mean (\pm SE) number of eggs in a Bell's vireo nest based on the response of the pair to parasitism by brown-headed cowbirds. Only pairs that had 2 or more nests parasitized within a season were included in this analysis. (a) Number of brown-headed cowbird eggs received in Bell's vireo nests. (b) Number of vireo eggs that remained in parasitized nests. Acceptor 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 ($P > 0.05$).

pairs. The mean number of vireo eggs that remained in a parasitized nest also differed among responses ($F_{3,262} = 249.30$, $P < 0.0001$; 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 antiparasite hypothesis because 3 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 nonforest 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 2 vireo eggs. In that case only, we saw a positive relationship between the number of cowbird eggs laid and probability of nest desertion. However, in vireo nests with 2 eggs remaining, between 0 and 3 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 2-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 6 times within a season (Budnik et al. 2001; KL Kosciuch, unpublished data). 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; unpublished data). However, the seasonal effects of date of clutch initiation on postfledging 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 antiparasite 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 that host species have not evolved antiparasite 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 (KL Kosciuch, personal observation). 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 ex-

posure 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 antiparasite 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 with Kus' (1999) study area in southern California. Based on route-level analyses of Breeding Bird Survey data (1989–1998), 162.4 and 216.3 cowbirds per 100 km surveyed were detected on 2 routes near our study area in Kansas (routes 38016 and 38019), whereas only 5.2 and 5.7 cowbirds per 100 km surveyed were detected on 2 routes (routes 14119 and 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 JT and Griffith JC 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 antiparasite behaviors in time scales relevant to management objectives because vireos do not possess explicitly antiparasitic behaviors. Thus, it is critical to understand the proximate mechanisms that cause nest desertion when developing management strategies for songbirds of conservation concern.

We thank Tracy Adamson, Jarrod Bowers, Tara Conkling, and Beth Ross for field assistance. Bill Jensen and Jim Rivers provided suggestions that improved the quality of the experimental design. Tracey Johnson, Jackie Nooker, Jack Cully Jr, and the Sandercock laboratory provided comments on previous versions of the manuscript. Funding for fieldwork and cowbird traps was provided by the National Science Foundation (NSF)—funded Konza Prairie Long-term Ecological Research program, a University Small Research Grant from Kansas State University, Kansas Ornithological Society, and a Sigma Xi grant-in-aid of research. K.L.K. and B.K.S. were supported by the Division of Biology at Kansas State University, and T.H.P. was supported by Kansas State University and by an NSF International Research Fellowship (INT-0202704). Research protocols were approved by the Institutional Animal Care and Use Committee at Kansas State University.

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