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Brood parasitism of Black-capped Vireos: frontline and post-laying behavioral responses and effects on productivity

Than J. Boves,^{1,2,5} Jinelle H. Sperry,³ Kristin Comolli,² and Patrick J. Weatherhead⁴

¹Department of Biological Sciences, Arkansas State University, Jonesboro, Arkansas 72401, USA

²Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana-Champaign, Illinois 61801, USA

³Engineer Research and Development Center, Champaign, Illinois 61826, USA

⁴Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana-Champaign, Illinois 61822, USA

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ABSTRACT. The cost of brood parasitism favors the evolution of host behaviors that reduce the risk or expense of being parasitized. Endangered Black-capped Vireos (*Vireo atricapilla*) have likely coexisted with brood-parasitic Brown-headed Cowbirds (*Molothrus ater*) for more than 10,000 yr, so it is likely that they have evolved anti-parasitic behaviors. We monitored naturally parasitized and non-parasitized vireo nests to evaluate factors that might explain parasitism risk and nest desertion behavior and also assessed whether behaviors that occurred after being parasitized improved reproductive output. Vireos reduced the risk of parasitism by initiating breeding early and nesting farther from open grasslands and edges of woody thickets. Post-laying, nest desertion was common (70% of parasitized nests) and increased with both the presence of at least one cowbird egg in nests and clutch reduction by cowbirds. After accounting for these cues, desertion was also more likely at nests located closer to cowbird foraging habitat and below potential cowbird vantage points. Despite its regularity, desertion did not appear to provide reproductive benefits to vireos. Instead, accepting cowbird eggs was a more effective strategy because 42% of cowbird eggs did not hatch. Furthermore, cowbird eggs were somehow ejected from at least three vireo nests. Our results suggest that Black-capped Vireos can behave in a variety of ways that reduce the impact of brood parasitism, with frontline behaviors appearing to provide the greatest benefit. Our results also suggest that habitat management should focus on providing Black-capped Vireos with adequate breeding habitat that provides access to safe nesting sites, and with high-quality wintering habitat that allows vireos to migrate and initiate nesting early.

RESUMEN. Parasitismo reproductivo en *Vireo atricapilla*: respuestas de conducta pre y post-puesta y su efecto en la productividad

El costo del parasitismo reproductivo favorece la evolución de la conducta del huésped para que de alguna manera reduzca el riesgo o el costo de ser parasitado. El Vireo (*Vireo atricapilla*) ha coexistido, por más de 10,000 años, con el Tordo pardo (*Molothrus ater*) que es un parásito reproductivo y es posible que haya desarrollado alguna conducta anti parasítica. Monitoreamos nidos no parasitados y otros parasitados para evaluar los factores que puedan explicar el riesgo parasítico y la conducta de abandonar el nido, y también si la conducta llevada a cabo, luego de ser parasitado un nido, mejora el rendimiento reproductivo. Los vireos reducen el riesgo de ser parasitados comenzando a reproducirse temprano y anidando lejos de herbazales abiertos y bordes de matorrales. El abandono de nidos, luego de la puesta, fue algo común (70% de los nidos parasitados) e incremento, con la presencia de al menos un huevo de tordo o la reducción de la camada de parte del parásito (remoción de huevos). Luego de tomar estas pistas en consideración, la probabilidad de deserción fue mayor en nidos más cercanos a las áreas de forrajeo de los tordos y bajo el potencial de ventaja de los tordos. Pese a su regularidad, la deserción de nidos no parece proveer de beneficio reproductivo a los vireos. El aceptar los huevos de tordo resultó ser una estrategia más efectiva porque el 42% de estos no eclosionaron. Más aun, los huevos de tordo fueron sacados del nido en al menos tres nidos de vireos. Nuestros resultados sugieren que los vireos pueden conducirse de varias formas que a su vez puede reducir el impacto de parasitismo reproductivo, y exhibir conductas novedosas que parecen proveer gran beneficio. Nuestros datos también sugieren que el manejo de hábitat debe enfocarse en proveer a los vireos de hábitat adecuado para anidar, de lugares más seguros para reproducirse y hábitat invernal de gran calidad, que le permita a estos migrar e iniciar temprano el anidamiento.

Key words: adaptive behavior, Brown-headed Cowbird, coevolution, *Molothrus ater*, nest abandonment, nest desertion, *Vireo atricapilla*

⁵Corresponding author. Email: tboves@astate.edu

Brood parasitism is often costly to hosts (Lowther 1993, Rothstein and Robinson 1998, Peer et al. 2005), favoring the evolution of host behaviors that reduce the risk or expense of being parasitized (Davies 2000, Peer et al. 2005). Frontline behaviors (those that occur prior to egg laying by a nest parasite) that help potential hosts avoid parasitism (Feeney et al. 2012) include choosing nest sites concealed from parasites (Patten et al. 2011), physically attacking parasites (Trnka et al. 2012), behaving inconspicuously (Clotfelter 1998), and shifting the timing of nesting to reduce breeding synchrony with parasites (Saino et al. 2010). Behaviors that can reduce the cost of parasitism once it has occurred include ejection of the parasite's eggs or nestlings (Rothstein 1975, Sato et al. 2010), burying parasitic eggs (Sealy 1995), and deserting parasitized nests (Hosoi and Rothstein 2000). Despite the costs of parasitism and the evolution of anti-parasite defenses in many birds, some host species appear to lack such defenses or only a portion of the population exhibits the behavior (Davies 2000, Kosciuch et al. 2006). Determining the extent to which a host species exhibits anti-parasitic behaviors has applications to conservation as well, particularly where brood parasites are thought to threaten the viability of the host species, because this information has implications for how to best manage vulnerable species.

Black-capped Vireos (*Vireo atricapilla*, hereafter vireo[s]) are considered vulnerable to extinction in large part due to the negative impact of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*, hereafter cowbirds; Grzybowski 1995, Kostecke et al. 2005). These two species have likely existed sympatrically for >10,000 yr because the vireo's distribution spans what is thought to have also been the historic range of cowbirds (Rothstein and Peer 2005). Thus, vireos may possess adaptations to combat brood parasitism. However, little is currently known about the anti-parasitic behaviors that vireos exhibit or how frequently they occur. Campomizzi et al. (2013) found that vireos could avoid parasitism by breeding early or late, but that nest site selection had little effect on the likelihood of being parasitized and that desertion after being parasitized was rare. Alternatively, Grzybowski (1995) described nest desertion as the only

anti-parasitic behavior of vireos, but little is known about the prevalence of desertion, the proximate factors that might elicit its expression, or how the behavior affects individual fitness. Nest desertion could be an adaptive response to parasitism triggered by the presence of a cowbird egg in a vireo's nest (Hosoi and Rothstein 2000), by generalized nest disturbances such as clutch reduction (Kosciuch et al. 2006), or by a combination of factors including interactions with adult parasites near nests (Graham 1988, Soler et al. 2012). Also, although nest desertion might be expected to improve fitness, this may not always be the case, particularly if subsequent nests are also parasitized (Kus 2002, Hoover et al. 2006). Furthermore, despite Grzybowski's (1995) assertion that vireos exhibit no other anti-parasitic behavior, no one to date has examined the possibility that they might exhibit additional anti-parasitic behaviors. Thus, our objectives were to assess vireo anti-parasitic defenses by: (1) identifying frontline (pre-laying) behaviors (e.g., nest site selection and nest timing) and associated parasitism rates, (2) determining the types and prevalence of post-laying behaviors that vireos display that may reduce the cost of being parasitized, (3) identifying the proximate factors that influence nest desertion to determine if parasitism alone is sufficient to explain patterns of desertion in this species, and (4) evaluating the consequences of alternative post-laying behavioral responses (desert or accept) on annual and 2-yr reproductive output.

METHODS

We conducted our study at the Fort Hood Military Reservation in central Texas (31°21'9"N, 97°47'40"W) during the spring and summer of 2011 and 2012. Vegetation in the study area was typical of vireo breeding habitat in the region, characterized by small thickets of early to mid-successional woody plants interspersed with herbaceous ground cover. Woody species composition was dominated by shin oak (*Quercus sinuata*), but included ashe juniper (*Juniperus ashei*), Texas red oak (*Quercus buckleyi*), Texas redbud (*Cercis canadensis*), and Texas ash (*Fraxinus texensis*). Although lethal cowbird control (via shooting and trapping) is ongoing on Fort Hood, our study area was located >9 km

from the nearest trapping station and no focused shooting had occurred on our site for at least 7 yr. Thus, we regularly observed cowbirds in the area, often associated with cattle that grazed both on and around the study area (primarily on grasslands scattered around the periphery of the site). We conducted daily surveys that covered the entire study area (~200 ha) for singing vireos beginning on 12 March of both years. When on territory, male vireos sing incessantly, which allowed us to conduct a census of male vireos on the study area. Once males and females settled on territories, we also captured and banded as many individuals as possible using mist nets and playback of vireo songs, male and female “shrads” (scolding calls), Eastern Screech-Owl (*Megascops asio*) vocalizations, and White-eyed Vireo (*Vireo griseus*) scold calls. We marked birds with unique combinations of colored and U.S.G.S. aluminum leg bands, sexed birds based on plumage or the presence of a brood patch (for females), and aged individuals as second-year (first breeding season) or after-second-year by molt limits (Pyle 1997). We measured mass (± 0.01 g) using a digital scale.

We located nests primarily by following vireo pairs and observing breeding-related behavior (e.g., courtship and nest-building). Courtship began at the end of March and nesting continued through July, with the latest brood fledging on 18 July. We monitored nests daily during building and laying and every 1–2 d during the incubation and nestling stages. On each nest check, we recorded the nest stage, nest contents, and current status. When nests were deserted or predated, we followed pairs to locate re-nesting attempts; we attempted to find all nests in as many territories as possible. We considered nests parasitized if we observed a cowbird egg in the nest (cowbird eggs are larger and heavily spotted and vireo eggs are almost completely white). We considered any vireo pairs that continued to lay or incubate eggs after parasitism to have accepted the cowbird egg(s). We determined the status of nests (active or deserted) by observing nest contents and parental behavior. When we observed no change in nest contents, but no parental activity at a nest, we placed a small leaf on the nest contents and returned later in the day to see if the leaf had been removed. If the leaf remained for multiple days with no sign of activity, we considered the nest deserted (from the day we placed the leaf). In some instances,

Table 1. List of variables evaluated hierarchically for inclusion in final models explaining the likelihood of parasitism, desertion, and predation of Black-capped Vireo nests at Fort Hood, Texas, 2011–2012.

Variable suite	Variable	Notation
I. Temporal	Year	YEAR
	Season (linear)	DATE
	Season (quadratic)	DATE ²
II. Habitat	Nest height	NHGT
	Distance to horizontal edge	DHOR
	Distance to vertical edge	DVER
	Lateral cover	LCOV
	Vertical cover	VCOV
	Distance to open grassland	DGRAS
III. Conspecific and individual	Vireo breeding density	VIDE
	Male age	MAGE
	Female age	FAGE
	Male mass	MASS
IV. Nest contents	Parasitized state ^{a,b}	PARA
	Cowbird eggs laid ^a	#BHCO
	Vireo eggs removed ^a	EGGR

^aIncluded in model selection for variables related to desertion.

^bIncluded in model selection for variables related to predation.

nests were parasitized before vireos began to lay eggs. We considered these nests active only if we observed vireos continuing to construct the nest post-parasitism or if evidence suggested that construction was already complete (i.e., lining added). If nests were found empty, we considered them to have been predated. When a vireo egg disappeared from a parasitized nest, but cowbird egg(s) remained, we assumed that a cowbird had removed the vireo egg (Scott et al. 1992, Sealy 1992, Peer 2006). While nest searching and monitoring, we assigned individuals to nests either by observing marked individuals at nests, or by inference (for males) based on the territory in which a nest was located. Because we were not able to associate individuals with all nesting attempts, sample sizes are reduced for nests with information about individual vireos.

Selection of predictor variables. To identify factors associated with parasitism risk, we compared a variety of temporal, habitat, conspecific, and individual variables chosen *a priori* (Table 1). One way for hosts to reduce

parasitism risk is to reduce breeding overlap with parasites (Saino et al. 2010, Feeney et al. 2012). Therefore, we determined whether the incidence of brood parasitism of vireos varied with timing of nesting. Temporal variables we included were year [YEAR] and season (Julian first egg date [DATE] and quadratic first egg date [DATE²]). Because habitat variables related to nest location and concealment may influence the ability of parasites to locate nests, we assessed the incidence of parasitism relative to variables that have been considered important in previous studies (Budnik et al. 2002, Lima 2009, Patten et al. 2011, Feeney et al. 2012). Our habitat variables included nest height [NHGT] and distance from nest to both the horizontal [DHOR] and vertical [DVER] edge of woody vegetation. On our study area, vireos nest within well-defined woody thickets that are interspersed with herbaceous vegetation, so we measured distance to edge by measuring from the edge of the nest cup to the closest break of foliage of woody plants (both horizontally and vertically from the nest). We also estimated lateral [LCOV] and vertical [VCOV] concealment by visually estimating the proportion of nests concealed by foliage or woody vegetation 1 m from nests. To estimate lateral cover, we calculated the harmonic mean of concealment, as opposed to arithmetic mean, at nest level from four measurements (in each cardinal direction) to better reflect situations where otherwise concealed nests are highly visible from one direction (which may affect vulnerability to parasitism or predation). Because harmonic means cannot be calculated with values of 0, we converted values of 0 to 1%. We also included the broader habitat measure of distance to open grassland (where cattle seemed to be most abundant) [DGRAS] using ArcGIS (Version 10.0, ESRI, Redlands, CA). Host breeding density can affect the probability of parasitism (Barber and Martin 1997, Campobello and Sealy 2011) and parental age or condition (body mass is typically as good or better at explaining variation in energy reserves than body size-adjusted indices; Schamber et al. 2009, Labocha and Hayes 2012) can influence nest-site selection or nest defense against parasites (Smith 1981, Montgomerie and Weatherhead 1988, Hogstad 2005), so we assessed their effects on the risk of parasitism. We did not calculate vireo breeding density, but used the number

of adjacent territories as a proxy [VIDE]. We considered territories adjacent if males were detected engaging in territorial behaviors (e.g., counter-singing) within 25 m of each other or if we observed males aggressively interacting. When available, we also included age (male: [MAGE] and female: [FAGE]) and mass (male only: [MASS]) of the vireos associated with a nest.

To identify variables related to nest desertion, we evaluated the same variables described above and also assessed the influence of nest contents. Nest content variables included the parasitized status of the nest (yes or no, [PARA]), number of cowbird eggs laid [#BHCO], and number of vireo eggs removed by cowbirds [EGGR]. The decision to desert may vary throughout the season because of changing re-nesting potential or because cowbird abundance or visibility varies seasonally (Boves, unpubl. data). Habitat variables may influence the density and visibility of cowbirds (or other predators) to parents, which may in turn influence the decision to desert (Guigueno and Sealy 2010). Age and condition of parents may influence the decision to desert because younger birds may be naïve to the effects of parasitism or need time to reliably recognize parasitic eggs (Lotem et al. 1992), and nest contents should influence the decision to desert if vireos recognize cowbird eggs (Davies 2000) or identify other types of disturbances at the nest (Kosciuch et al. 2006).

Finally, we evaluated the influence of the same variables on nest predation to determine if reducing the risk or cost of parasitism for vireos might be constrained by increased risk of predation. We considered the same predictor variables as parasitism, but also included the parasitized state of a nest [PARA] as a potential predictor of predation because cowbird nestlings may attract predators directly via increased begging (Hoover and Reetz 2006) or indirectly by affecting parental defense or provisioning activity (Tewksbury et al. 2002).

Statistical analyses. We constructed general linear models with a binomial distribution and a logit link function and compared models using an information theoretic framework to identify behaviors or other factors that best explained patterns of parasitism, nest desertion, and predation (performing separate analyses for each dichotomous response). We did not use logistic exposure for predation analysis because

we are confident that we were able to locate a large proportion of all nesting attempts (>90%) soon after initiation of building and intervals between nest visits were typically only 1 d. Before performing analyses, we assessed collinearity among variables by examining Pearson's pairwise correlations. No variables were strongly correlated (all $r < 0.4$). We standardized all continuous input variables by subtracting the mean and dividing each value by two times its standard deviation, as recommended by Gelman (2008), so that all resulting parameter estimates were directly comparable, including those for binary predictors.

We compared models based on Akaike information criterion values corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002). To reduce the total number of models, we compared and reduced complexity of the most highly parameterized models, and we performed variable selection in a hierarchical manner (Table 1). To identify factors associated with parasitism, we first assessed all possible additive and interactive temporal variables (six candidate models). We then carried all models with ΔAIC_c values ≤ 2 (which indicates equivalence among models) over to the next suite of variables that included habitat measurements and conspecific density. Here, we again assessed all possible additive models as well as interactions with any remaining temporal variables. Because we were only able to identify individual vireos at a subset of total nests, we performed model selection separately for those nests. We again performed model selection as described above, but then carried over the top candidate models to a suite of variables that included minimum male age and male body mass. For an even further reduced subset of nests (where we captured and identified females), we repeated this process and incorporated female age as a potential predictor in the final step.

To identify factors associated with desertion behavior, we followed a similar process but added the suite of variables that included nest contents after assessing temporal and habitat variables. In this case, we included all nests that were not predated during egg laying or within the first 4 d of incubation. Finally, to identify factors associated with predation (and compare them with those associated with parasitism risk), we followed the same approach used for parasitism, but excluded deserted nests. In

each instance of model selection, we compared candidate models with a null model (intercept only).

We calculated Akaike weights for all of the equivalent models in each final model set ($\Delta AIC_c \leq 2$) and assessed the influence of variables included in these models by examining parameter estimates and 95% CI derived by model averaging. We used the natural average method, where parameter estimates are averaged only from models that contained the variable of interest (Burnham and Anderson 2002). We were unable to perform model selection using male identity as a random effect because some highly parameterized models failed to converge when doing so. We assessed the fit of each top model using a χ^2 goodness of fit test.

To evaluate the reproductive consequences of alternative behavioral responses to parasitism (desert or accept), we used non-parametric Wilcoxon tests to compare the fecundity (number of fledglings produced) that resulted after each behavior on (1) an annual basis (i.e., from that nest and all subsequent nests within the individual's territory) and, for those birds parasitized during the first season, (2) across two breeding seasons. We considered the decision (desert or accept) made at each parasitized nest to be the sampling unit and, because of this, some individuals had multiple decisions included in the analysis. We ensured that this potential lack of independence among samples did not affect our inferences by performing a separate analysis where we restricted the analysis to only the initial parasitized nest of an individual. The results were qualitatively unchanged so we used the full complement of nests in our final analysis to provide more power to detect statistical differences. We limited our analyses to decisions made at nests in the territories of males where we were confident we located all nesting attempts, and thus have an accurate estimate of fecundity (seasonal and over 2 yr) subsequent to decisions to accept or desert. We used males to estimate fecundity because we did not know the identity of females at a large number nests, and we expect that male estimates approximate those of females. Finally, we felt that if desertion was adaptive within years, a vireo that deserted a parasitized nest must have the opportunity to re-nest that year. Therefore, for the 1-yr analysis, we excluded three nests parasitized late in the season when we estimated it would have been

too late to re-nest given the nesting phenology of the population. If desertion is adaptive over a longer time scale, it may be because desertion increases the likelihood of nesting successfully the following year; thus, we included those three nests for the analysis over 2 yr. We used JMP (Version 10.0, SAS Institute, Cary, NC) and SAS (Version 9.3, SAS Institute) for statistical analyses.

RESULTS

We located and monitored 143 vireo nests where ≥ 1 egg (vireo or cowbird) was laid. We found cowbird eggs in 90 nests (63%) and, at one nest, a cowbird egg was discovered directly below the nest. Of 53 non-parasitized nests, 21 fledged vireo young (39.6%). Of 90 parasitized nests, seven fledged vireo young (7.7%) and three fledged cowbird young (3.3%). We were able to determine a behavioral response to parasitism at 79 of 90 parasitized nests; 11 nests were excluded because vireos did not complete nest construction or nest contents were predated (or the nest was destroyed) before we could determine behavior. Of these 79 nests, 55 were deserted (70%), 22 parasitized clutches were accepted (28%), and a cowbird egg was removed after being laid at three nests (4%). In addition, four non-parasitized nests were deserted (without being predated). In total, we documented 110 cowbird eggs in vireo nests, with multiple parasitisms in 18 nests ($\bar{x} = 1.22 \pm 0.05$ cowbird eggs laid/parasitized nest; range = 1–3 cowbird eggs). We inferred cowbird removal of vireo eggs at 30 nests (33%) and, based on missed laying days, eggs may have been removed in as many as 18 additional nests (thus affecting up to 53% of parasitized nests). Forty nests, regardless of parasitized state, were predated (28%; does not include partial clutch/brood loss putatively caused by cowbirds).

Factors associated with parasitism. For the complete set of nests, 10 models were equivalent at explaining the likelihood of parasitism (Table 2). These models consistently contained six variables, including year, first egg date, quadratic first egg date, distance to grassland, distance to grassland*year, and distance to horizontal edge, with only slight variations (Table 2). The top model fit the data well ($\chi^2_{136} = 142.1$, $P = 0.35$). Variables strongly associated with the likelihood of parasitism (i.e., 95% CI did

Table 2. Top models explaining the probability of brood parasitism of Black-capped Vireo nests ($N = 143$). See Table 1 and text for model variable descriptions. Models derived using the complete data set. K refers to the number of parameters in the model. AIC_c weights (w) refer only to models that garnered strong support ($\Delta AIC_c \leq 2$ displayed here) and null models (see Table S1 for reduced sample model sets).

Final models	K	AIC_c	ΔAIC_c	w	R^2
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+DHOR	7	148.47	0.00	0.14	0.29
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+DHOR+VCOV	8	148.87	0.40	0.11	0.30
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR	6	148.89	0.42	0.11	0.28
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+DHOR+VIDE	8	149.29	0.82	0.09	0.30
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+VIDE	7	149.30	0.83	0.09	0.30
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+DHOR+DVER	8	149.63	1.16	0.08	0.30
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+DHOR+VCOV+VIDE	9	149.84	1.37	0.07	0.31
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+DVER	7	150.09	1.63	0.06	0.28
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+VCOV	7	150.09	1.63	0.06	0.28
YEAR+DATE+DATE ² +DGRAS+DGRAS*YEAR+DHOR+DVER+VIDE	9	150.23	1.76	0.06	0.31
Intercept only (Null)	1	190.59	42.12	0.00	0.00

Table 3. Parameter estimates, and associated 95% CI, for variables associated with the likelihood of parasitism, desertion, and predation of the nests of Black-capped Vireos. Estimates were derived by model-averaging (using the natural average method) from models with $\Delta AIC_c \leq 2$. Estimates displayed are from analysis of full data set unless variable was not present in any equivalent model from the full set (indicated by superscript), or inference was changed by inclusion of male or female traits (e.g., sign reversal). Variables found in models only when assessing reduced samples are displayed only if male or female traits were also included in the model. The β estimates for variables marked with (#) may not be meaningful because of involvement with compound effects. Results in bold indicate that 95% confidence intervals did not include zero.

Variable	β	95% CI lower	95% CI upper
Parasitism			
Year (2011) ^a	0.35	-0.06	0.76
First egg date (#)^a	1.98	1.20	2.85
First egg date^{2a}	-2.62	-4.27	-1.07
Distance to grassland (#) ^a	-0.80	-1.77	0.09
Distance to grassland*year^a	1.06	0.28	1.95
Distance to horizontal edge ^a	-0.83	-1.82	0.12
Conspecific density ^a	0.20	-0.11	0.54
Distance to vertical edge ^a	0.07	-0.06	0.22
Vertical cover ^a	-0.52	-1.39	0.31
Male mass (#) ^b	-0.54	-1.68	0.55
Male mass*date^b	3.83	1.15	7.00
Desertion			
Year (2011)^a	0.87	0.28	1.53
First egg date^a	1.18	0.07	2.39
Parasitized (Y)^a	0.82	0.04	1.54
Vireo eggs removed^a	4.38	2.03	8.00
Distance to grassland^a	-1.93	-3.46	-0.60
Distance to vertical edge^a	1.61	0.29	3.27
Distance to horizontal edge (#) ^a	-1.05	-2.70	0.54
Distance to horizontal edge*year^a	1.70	0.19	3.46
Vertical cover (#) ^a	-0.14	-1.44	1.14
Vertical cover*year ^a	1.63	0.31	3.12
Male age (#)^b	-2.08	-4.58	-0.44
Male age*date ^b	1.19	-0.35	3.66
Predation			
Year (2011)^a	0.79	0.25	1.40
Distance to vertical edge (#) ^a	0.97	-0.14	2.27
Distance to vertical edge*year ^a	0.80	-0.51	2.34
Harmonic lateral cover (#) ^a	-0.64	-1.85	0.46
Harmonic lateral cover*year ^a	-1.06	-2.27	0.03

^aEstimates derived from models using complete data set (no male or female traits).

^bEstimates derived from models using reduced data set (including male traits).

not overlap zero; Table 3) included first egg date, with nests initiated early in the breeding season less likely to parasitized (Fig. 1A) and, in 2012, distance from grassland, with nests farther from grasslands less likely to be parasitized (but this differed by year; Fig. 1B). Nests located farther from horizontal edges were also less likely to be parasitized, but this relationship was not as strong (95% CI included zero; Fig. 1C). When only nests where we had information about males were included

($N = 123$), four models were equivalent. Most models included the same variables from above and inferences concerning these variables were unchanged, but, in addition, male mass and male mass*date were included (Table 2) and distance to horizontal edge was more strongly associated ($\beta = -1.34$; 95% CI = -2.47 to -0.28). The inclusion of male mass*date indicated that nests of heavier males were less likely to be parasitized, but only early in the nesting season (Fig. 1D). Female age did not affect the

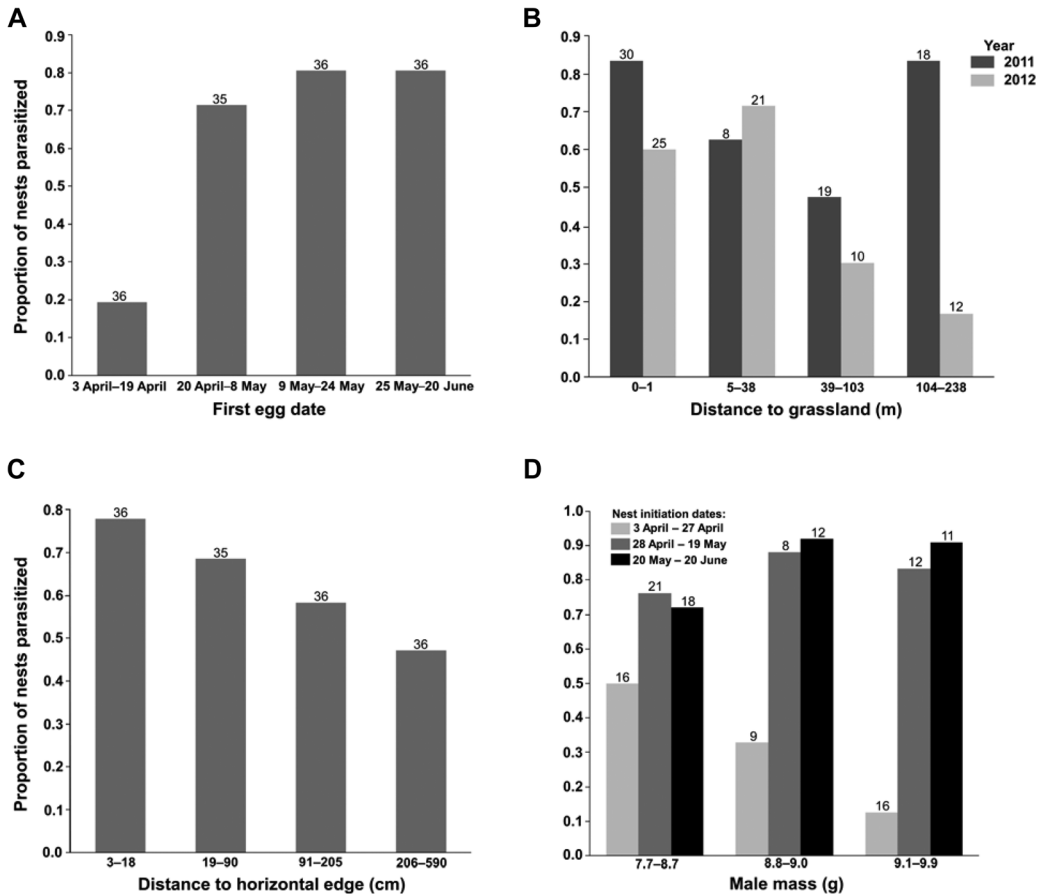


Fig. 1. Proportion of Black-capped Vireo nests parasitized (based on raw data) as a function of variables included in top models (see Table 2) and strongly associated with the probability of parasitism (i.e., 95% CI of β estimate did not include 0; see Table 3). Strongly associated variables from the full-nest sample included (A) first-egg date, (B) distance from nest to grassland (by year), and (C) distance from nest to horizontal edge. An additional influential variable from the reduced data set was (D) male mass (by date). Sample sizes are indicated above bars and refer to the total number of nests within the respective bin.

probability of parasitism (see Table S1 for a complete list of top models using reduced data sets).

Factors associated with nest desertion. For the complete set of nests, four models were equivalent at explaining the likelihood of nest desertion (Table 4). Six factors were consistently included in top models (Table 2). Desertion was higher in 2011, increased with nest initiation date (Fig. 2A), was higher in parasitized nests, increased with the number of vireo eggs removed (Fig. 2B), increased with proximity to grasslands (Fig. 2C), and increased with distance from vertical cover (Fig. 2D). The top model fit the

data well ($\chi^2_{105} = 83.6$, $P = 0.94$). In the analysis of nests where we had information about males, four models were equivalent at explaining nest desertion. Again, the same variables from above were important and inferences concerning these variables were unchanged, but male age was also influential (Table 2). Nests of younger males were more likely to be deserted (Fig. 2E). Female age did not affect the probability of desertion (see Table S2 for a complete list of top models using reduced data sets).

Factors associated with predation. For the complete set of nests, four models were equivalent at explaining the likelihood of

Table 4. Top models explaining the probability of nest desertion by Black-capped Vireos ($N = 112$ nests). See text for model variable descriptions. Models derived using the complete data set. K refers to the number of parameters in the model. AIC_c weights (w) refer only to models with strong support ($\Delta AIC_c \leq 2$ displayed here) and null models. See Table S3 for reduced sample model sets.

Final models	K	AIC_c	ΔAIC_c	w	R^2
YEAR+DATE+PARA+EGGR+DGRAS+DVER	7	105.80	0	0.22	0.40
YEAR+DATE+PARA+EGGR+DGRAS+DVER+DHOR+ DHOR*YEAR+ VCOV+VCOV*YEAR	11	106.43	0.63	0.16	0.46
YEAR+DATE+PARA+EGGR+DGRAS+DVER+DHOR	8	106.61	0.81	0.15	0.42
YEAR+DATE+EGGR+DGRAS+DVER+DHOR+DHOR*YEAR+ VCOV+VCOV*YEAR	10	107.54	1.74	0.09	0.40
Intercept only (Null)	1	152.95	47.15	0.00	0.00

predation, and only year was strongly associated with the likelihood of predation (predation rates were higher in 2011; Table 3). However, the top model did not fit the data well ($\chi^2_{63} = 82.9, P = 0.05$). No male characteristics were associated with the likelihood of predation (from the reduced sample), and female age was only weakly related to a decreased likelihood of predation (present only in the fourth-ranked model and 95% CI included zero; Table 3; see Table S3 for a complete list of top models).

Reproductive consequences of acceptance versus desertion. Despite the regularity of nest desertion behavior, desertion resulted in lower fecundity (fledglings/male territory) than acceptance for both 1-yr (desertion: $0.34 \pm 0.15, N = 44$; acceptance: 0.91 ± 0.29 ; $Z = 2.3, N = 22, P = 0.02$; non-parasitized: $1.69 \pm 0.28, N = 51$) and 2-yr fecundity estimates (desertion: $0.78 \pm 0.26, N = 11$; acceptance: $2.82 \pm 0.72, N = 32$; $Z = 3.1, P = 0.002$). Greater fecundity with acceptance of parasitized clutches was due to a substantial number of cowbird eggs failing to hatch. Nine of 21 cowbird eggs (in 19 singly parasitized nests and two multiply parasitized nests with two cowbird eggs) incubated for the appropriate time period failed to hatch (42%); all parasitized nests that fledged vireo young contained cowbird eggs that failed to hatch.

DISCUSSION

Our data demonstrate that Black-capped Vireos engage in pre-laying behaviors that can reduce the risk of brood parasitism. Post-laying, nest desertion was influenced by parasitism status and several other variables potentially related to the presence of adult cowbirds near nests. However, under the repeated parasitism pressure experienced by these vireos, desertion did not provide reproductive benefits. Furthermore, behaviors that reduced the risk or cost of parasitism did not appear to affect predation risk.

Behavior limiting brood parasitism. Studies of anti-parasitic behavior of host species have overwhelmingly focused on the post-laying period, even though behaviors that reduce the risk of parasitism are likely to confer the greatest fitness advantage (Patten et al. 2011, Feeney et al. 2012). We found that vireos can behave in ways that decrease the probability of being parasitized, with early nesting being the most

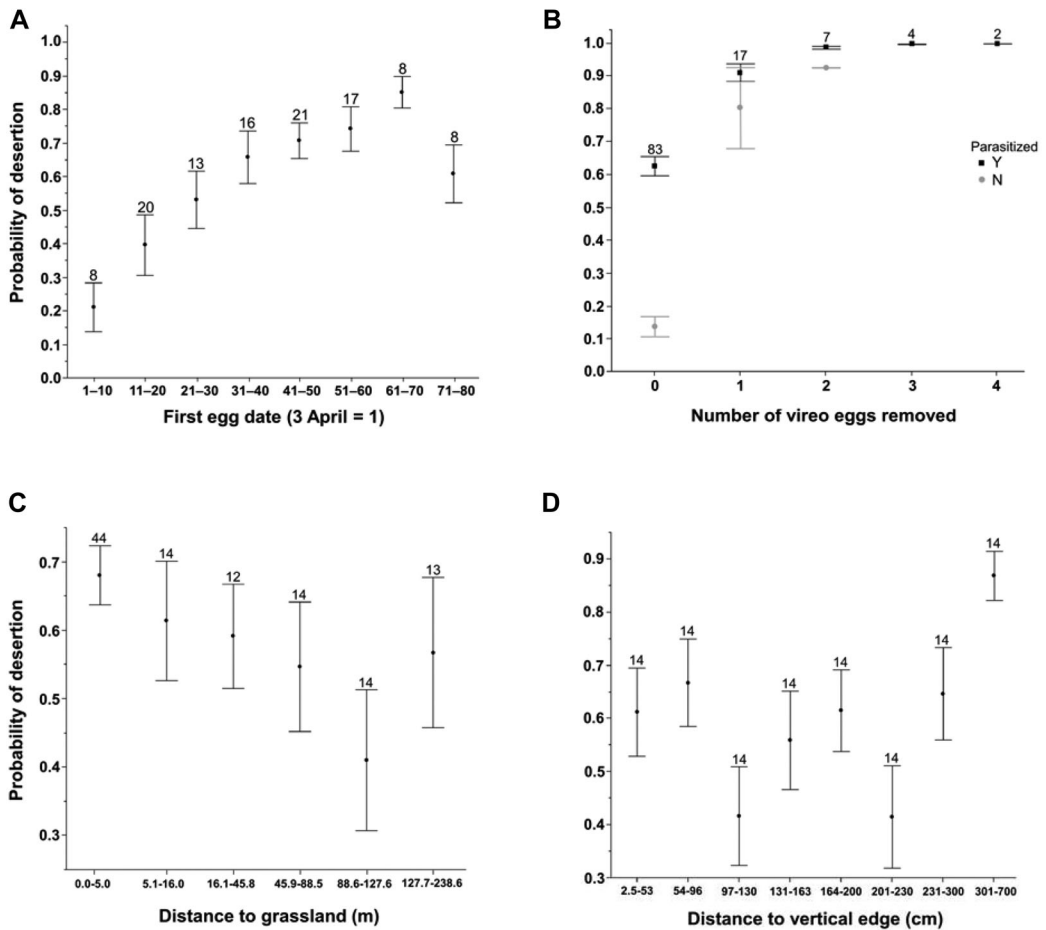


Fig. 2. Probability of nest desertion by Black-capped Vireos as a function of variables that were included in top models and strongly associated with the probability of desertion (i.e., 95% CI of β estimate did not include 0; see Table 2). Strongly associated variables from the full nest sample included (A) first egg date, (B) number of vireo eggs removed and parasitism status, (C) distance from nest to grassland, and (D) distance from nest to vertical edge. An additional strongly associated variable from the reduced data set was (E) male age. Points represent mean predicted probability ($\pm$ SE) of nest desertion for that range of values derived from the top model in which each variable was included. Sample sizes are indicated above bars and refer to the total number of nests within the respective bin.

potent of these behaviors. Similar results were reported in a previous study of Black-capped Vireos (Campomizzi et al. 2013) as well as in studies of other host species (Strausberger 1998, Hoover et al. 2006). No vireo nests initiated before 15 April were parasitized (with the exception of two nests parasitized during the nestling stage), presumably because cowbirds in this region often do not start laying until mid-April (Summers, pers. comm.). Vireos that arrived on the breeding grounds first also

initiated breeding earliest (Boves, unpubl. data), so avoiding brood parasitism can be added to the list of benefits of early migration for songbirds (Kokko 1999, Smith and Moore 2005, Møller et al. 2008). We found no evidence that a trade-off with predation existed (e.g., if early nests suffered higher predation rates), and other research has also shown that early vireo nests avoid predation by snakes (Sperry et al. 2008). Therefore, increased risk of predation should not constrain selection favoring earlier nesting, but

other factors (e.g., weather and food availability) could do so.

The potential for vireos to migrate and start nesting earlier is unknown, although the timing of migratory behavior of other species is largely genetically controlled (Berthold 1998). However, it also appears that in many species enough variation exists to allow population-wide phenological shifts to occur over short time periods (Pulido et al. 2001). This is particularly true for short-distance migrants like vireos. If conditions in wintering areas are appropriate, birds may be able to migrate and initiate breeding even earlier (Marra et al. 1998). Shifts in breeding timing by vireos could select for earlier breeding by cowbirds, but this seems unlikely because cowbirds are generalist parasites.

In addition to phenological mismatching, we found that nests located farther from cowbird vantage points (i.e., horizontal edges of woody thickets) and foraging habitat (open grasslands, but this relationship was present only in 1 yr) were less likely to be parasitized. Cowbirds typically travel relatively short distances (<2 km) between adjacent breeding and foraging grounds (Goguen and Mathews 2001), suggesting that nests further from cattle grazing may be less vulnerable. The advantage of nesting farther from horizontal edges was consistent between the two years and has also been documented for other host species (Freeman et al. 1990, Johnson and van Riper 2004, Patten et al. 2011). Previous investigators reported that no habitat variables related to the likelihood of vireo nests being parasitized (Barber and Martin 1997, Campomizzi et al. 2013). One possible reason for our differing results is that Barber and Martin (1997) conducted their study in areas where cowbird numbers were being controlled (only 29% of nests were parasitized), and the smaller sample of parasitized nests could have made it less likely that a strong relationship could be found. In addition, although Campomizzi et al. (2013) documented parasitism rates similar to ours (72%), their total sample of nests was relatively small ($N = 38$ over 3 yr). They also concentrated on broader-scale habitat metrics and did not include micro-habitat features that could provide safe refuge from brood parasitism. Interestingly, nest desertion was also rare in their study, suggesting that their nest searching efforts may not have been as intensive as ours and that nests were often found at later nesting stages

(post-incubation). Thus, their data may have consisted of a biased sample, missing the most inconspicuous nests (which may also be the most difficult for cowbirds to locate); without this subset, no habitat relationships were inferred.

As with the timing of nest initiation, habitat features advantageous with respect to parasitism generally did not affect predation risk, although our 2-yr study could have missed temporal heterogeneity in what constitutes a safe nest site (Chalfoun and Schmidt 2012). What is also unknown is whether nest locations with "safe" characteristics are limited. It is possible that most individuals would prefer to nest in parasite-safe locations, but, if excluded from such locations, some pairs may have to resort to using more parasite-prone nest sites.

We found little influence of individual characteristics on the likelihood of parasitism. The only trait associated with decreased parasitism was male mass, and the importance of mass was dependent on time of year (larger birds were parasitized less often, but only early in the breeding season). During egg-laying, male vireos often sit on eggs (Grzybowski 1995), which may provide defense of nest contents in the form of camouflage or as vigilance against predators or brood parasites. If males in poor condition spend more time foraging early in the season, it may be at the expense of nest defense (Martin 1992, Komdeur and Kats 1999) or providing camouflage for high-contrast eggs. We do not know if physical defense plays a role in reducing parasitism of vireo nests, but such defense has been reported in other host species (e.g., Welbergen and Davies 2009), including Bell's Vireos (*Vireo bellii*; Ellison and Sealy 2007, but see Sharp and Kus 2004).

Post-laying behaviors and proximate factors explaining nest desertion. Vireos were more likely to desert nests when parasitized, even when controlling for factors that could explain desertion behavior. Thus, unlike Bell's Vireos (Kosciuch et al. 2006), it appears that nest desertion by Black-capped Vireos was not simply a response to clutch reduction and that multiple factors affect the probability of desertion. We found that nests initiated later in the season when cowbirds are more abundant (Boves, unpubl. data), nests located closer to open grasslands where cowbirds forage (Lowther 1993), and nests located below taller vegetation, which may serve as vantage points for cowbirds,

were all more likely to be deserted. Other host species have also demonstrated sensitivity to the perceived risk of brood parasitism and some have been shown to require interactions with adult brood parasites, rather than the mere presence of parasitic eggs in the nest, to induce post-laying anti-parasitic behavior in species that desert nests (Guigueno and Sealy 2011) or reject parasitic eggs (Bártol et al. 2002, Soler et al. 2012). Also supporting this interpretation of the data was that there was often a lag between parasitism or egg removal and subsequent nest desertion; 19 nests were deserted more than 2 d after these potential triggers occurred, suggesting that some other cue(s) provided the final stimulus for desertion.

Despite its prevalence, desertion did not appear to be reproductively advantageous to vireos, and similar results have been reported for Least Bell's Vireos (*Vireo bellii pusillus*, Kus 2002), Prothonotary Warblers (*Protonotaria citrea*), and Red-winged Blackbirds (*Agelaius phoeniceus*, Hoover et al. 2006). Nest desertion would likely be adaptive if replacement nests were not parasitized or predated, but in areas with high parasitism rates, particularly during the peak of the breeding season, that may rarely occur (unless artificially created via cowbird or predator control). In fact, of 18 territories where desertion was the sole response to parasitism in our study, only one territory subsequently produced any vireo fledglings. Thus, the principal reason that acceptance was a more effective response to parasitism (than desertion) was that several cowbird eggs failed to hatch. One possible reason why vireos so often responded to parasitism by deserting their nests if it was disadvantageous to do so is that desertion provides other advantages, such as increased lifetime reproductive output or increased survival rates of adults or fledglings. This seems unlikely, however, because vireos that deserted nests in our study attempted to re-nest up to five times after deserting initial nests (thus expending a lot of energy and, even when successful, fledging broods late in the season). Another possibility is that desertion behavior has increased in the population because individuals more prone to desertion have been selected for over evolutionary time (including a time period when cowbirds were less sedentary or found at lower densities). If individuals are likely to be parasitized only once, desertion would likely be

an adaptive response. However, when exposed to repeated brood parasitism throughout the breeding season, these same individuals behave maladaptively by continuing to desert (Hoover et al. 2006).

Another possibility is that some vireos accepted cowbird eggs because they had some ability to reduce the hatching success of those eggs, perhaps by modifying their incubation behavior. Hatching rate data support this possibility, that is, for eggs laid during the appropriate period (i.e., before incubation began), cowbird eggs had a hatching rate of 58%, whereas vireo eggs incubated in parasitized clutches had a hatching rate of 74% (32/43). Typically, hatching rates of brood parasite eggs are similar to those of host eggs (Wiley 1986, Marvil and Cruz 1989, Clotfelter and Yasukawa 1999) or even higher in the nests of smaller hosts because cowbird eggs may disrupt incubation in these species (McMaster and Sealy 1998). Because the benefits of desertion are minimal under the pressure of repeated parasitism, altered incubation behavior may be an adaptive response to ease the negative effects of brood parasitism and make acceptance a better strategy. Assessment of these possibilities will require further investigation.

We also monitored three nests where cowbird eggs were ejected and one nest where we found a cowbird egg below the nest. In one of these cases, a vireo egg was also found beneath the nest, but, in the other two, no vireo eggs were removed. No previous evidence has indicated that vireos eject parasitic eggs. The intact state of removed eggs rules out puncture ejection and vireos' tomlial length does not appear great enough to grasp eject cowbird eggs (Rasmussen et al. 2010). Thus, if vireos removed the eggs, they must have used some other method, such as the recently discovered kick-ejection technique (De Mársico et al. 2013). Alternatively, other cowbirds may have removed these eggs prior to laying their own, although new cowbird eggs were never laid in these nests, ejected cowbird eggs were not damaged (cowbirds often puncture host eggs), and, other than one case of a cowbird eating a conspecific's egg (Benson 1939), we were unable to find documentation of such behavior. Interestingly, two parasitic egg removal events occurred in the same male territory and likely involved the same female vireo.

We found little evidence for the influence of parental age on probability of parasitism

although we did find a relationship between male age and likelihood of nest desertion. Younger males may be more likely to desert nests because they may have greater future reproductive (or survival) potential (Székely et al. 1996) than older birds. Other studies have provided mixed results concerning the effect of age on parasitism risk and responses. Lotem et al. (1992) found that young female Great Reed Warblers (*Acrocephalus arundinaceus*) accepted Common Cuckoo (*Cuculus canorus*) eggs more often than older females, and Smith (1981) found that older female Song Sparrows (*Melospiza melodia*) were parasitized more often than young breeders.

Conservation and management implications. Black-capped Vireos can behave in a variety of ways that reduce the risk of being parasitized and, after being parasitized, vireos may produce successful nests when cowbird eggs fail to hatch or are removed (however, desertion did not increase productivity in this cowbird-dense landscape). Thus, creating conditions that allow for the expression and spread of existing advantageous reproductive behaviors may be useful as a long-term, landscape-scale, conservation strategy. In its current exhaustive form, lethal cowbird control may reduce the likelihood that these beneficial behaviors would spread, and thus may be helping to maintain the long-term susceptibility of vireos to parasitism (e.g., Wilsey et al. 2014). Therefore, in the short and perhaps medium term, a potential management strategy that may hold promise, but will require testing, is to reduce cowbird control to a level that maintains cowbird parasitism as a selective pressure on vireo nesting behavior, but at an intensity that allows vireo populations to sustain themselves and does not put vireo populations at risk of stochastic events that could lead to extinction. Determining the optimal intensity of control will also require further investigation, but a maximum parasitism rate of 30%, based on population modeling efforts, was recently suggested as a level at which local vireo populations maintain themselves (Smith et al. 2013). Whatever level of cowbird control is implemented, it should be coupled with habitat management aimed at providing vireos with adequate breeding habitat to allow them access to safe nesting sites and high quality wintering habitat that allows vireos to migrate and initiate nesting early.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Top models explaining the probability of brood parasitism of Black-capped Vireo nests using reduced data sets that included male and female traits.

Table S2. Top models explaining the probability of desertion of Black-capped Vireo nests using reduced data sets that included male and female traits.

Table S3. Top models explaining the probability of predation of Black-capped Vireo nests. See text for model variable descriptions.