

FREQUENT VOCALIZING IS NEGATIVELY ASSOCIATED WITH BROOD PARASITISM IN A HOST OF THE BROWN-HEADED COWBIRD

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Abstract. Brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) can substantially affect host species' reproductive success. The "host-activity" hypothesis suggests that parasites eavesdrop on conspicuous behaviors to locate and parasitize hosts, and several studies of cowbird hosts support this hypothesis. In contrast, a recent study of the Least Bell's Vireo (*Vireo bellii pusillus*) reported a negative association between the host's vocalization rate near the nest and brood parasitism. This contradictory pattern is intriguing because Bell's Vireo is a common cowbird host and vocalizes near and on its nests. We tested a key assumption of the host-activity hypothesis in a different subspecies (*V. b. arizonae*) to determine whether the contradictory pattern reported in *V. b. pusillus* is an anomaly or could be generalized to other subspecies. Unparasitized vireos vocalized more frequently than parasitized birds, confirming that the pattern in Bell's Vireos is the opposite of that reported for other cowbird hosts. Nesting stage played a role: unparasitized birds vocalized more than parasitized birds only during the nest-building and incubation stages. Given that vocalization rate and other behaviors change through the breeding season, future tests of the host-activity hypothesis should control for nesting stage. Moreover, future efforts to identify the underlying cause for the association between vocalization rate and probability of parasitism should consider the possibility of reciprocal causal relationships between them. We propose five additional hypotheses to explain why in Bell's Vireo the pattern between these two traits is opposite of what has been reported in other birds.

Key words: Bell's Vireo, brood parasitism, Brown-headed Cowbird, eavesdropping, host-activity hypothesis, host behavior, *Molothrus ater*, *Vireo bellii*, vocalization rate.

Vocalización Frecuente Es Asociada Negativamente con el Parasitismo de Cría en un Hospedador de *Molothrus ater*

Resumen. El parasitismo de cría por parte de *Molothrus ater* puede afectar sustancialmente el éxito reproductivo de las especies hospedadoras. La hipótesis de "la actividad del hospedador" sugiere que los parásitos observan los comportamientos para localizar y parasitar al hospedadero. Varios estudios sobre los hospedadores de *M. ater* apoyan esta hipótesis. En contraste, un estudio sobre *Vireo bellii pusillus* mostró una asociación negativa entre la tasa de vocalización del hospedador cerca del nido y el parasitismo de cría. Este patrón contradictorio es intrigante porque *V. b. pusillus* es un hospedador común de *M. ater* y vocaliza en el nido y sus cercanías. Pusimos a prueba un punto clave de la hipótesis de la actividad del hospedador en una otra subespecie (*V. b. arizonae*) para determinar si el patrón contradictorio observado en *V. b. pusillus* es una anomalía o puede ser generalizado a otras subespecies. Los individuos de *V. b. arizonae* no parasitados vocalizaron más frecuentemente que los parasitados, lo que confirma que el patrón en *V. b. pusillus* es lo opuesto a lo reportado para otras especies hospedadoras de *M. ater*. La etapa de anidación fue importante: las aves no parasitadas vocalizaron más que las parasitadas sólo durante las etapas de construcción del nido y durante la incubación. Dado que la tasa de vocalización y otras conductas cambian a través de la temporada de cría, pruebas futuras sobre la hipótesis de actividad del hospedador deben controlar el estadio del nido. Por otra parte, los futuros esfuerzos para identificar la causa subyacente de la asociación entre la tasa de vocalización y la probabilidad de parasitismo deben considerar la posibilidad de relaciones recíprocas causales entre ellas. Proponemos cinco hipótesis adicionales para explicar por qué en *V. bellii* el patrón entre estos dos rasgos es lo opuesto a lo que ha sido reportado en otras aves.

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INTRODUCTION

Many avian species have evolved elaborate behavioral traits to communicate with conspecifics (Alcock 2001). In passerines, vocalizations are hypothesized to attract mates and repel rivals from territories (Searcy and Andersson 1986, Kroodsma and Byers 1991, Catchpole and Slater 2008). In many species, vocalization rate is positively correlated with mating success (Payne and Payne 1977, Gottlander 1987, Radesater et al. 1987, Alatalo et al. 1990) and can provide females with reliable indicators of males' quality (Zahavi 1975, Searcy 1979, Greig-Smith 1982). Avian vocalizations represent public information, and conspecifics may sometimes use such inadvertent cues to their benefit (Danchin et al. 2004, Betts et al. 2008). Similarly, other species may exploit these signals to enhance their own fitness (McGregor 1993, Bradbury and Vehrencamp 1998). For example, avian brood parasites may eavesdrop on the behaviors of potential hosts to help locate their nests (Clotfelter 1998, Banks and Martin 2001). Brood parasitism can have negative consequences for hosts' fitness, so selection should favor hosts' evolving defensive strategies aimed at reducing such costs (Rothstein 1975, 1990). Indeed, interactions between brood parasites and their hosts have been referred to as an evolutionary arms race, in which host behaviors that increase risk of brood parasitism undergo rapid evolutionary change, particularly in those species most negatively affected by brood parasitism (Davies et al. 1989, Rothstein 1990).

Understanding factors that influence the risk of brood parasitism is important from both evolutionary and conservation perspectives, and these factors have been the focus of extensive study (Brittingham and Temple 1983, Barber and Martin 1997, Clotfelter 1998, Tewksbury et al. 1998, Garamszegi and Avilés 2005). Recent research has examined the influence of host behavior on probability of parasitism (Gill et al. 1997, Grief and Sealy 2000, Garamszegi and Avilés 2005, Sharp and Kus 2006, Svagelj et al. 2009). The "host-activity" hypothesis (Clotfelter 1998, Banks and Martin 2001) suggests that frequent vocalizing near the nest increases risk of brood parasitism because brood parasites eavesdrop on hosts to locate and parasitize their nests (Clotfelter 1998, Banks and Martin 2001). The host-activity hypothesis is intriguing to evolutionary biologists because it suggests that a high rate of vocalization, while favored by sexual selection (Searcy and Andersson 1986), may concomitantly increase risk of brood parasitism, creating a trade-off between the benefits and costs of vocal communication.

Many studies have found support for the host-activity hypothesis, but one recent study reported the opposite pattern: unparasitized Least Bell's Vireos (*Vireo bellii*) vocalized nearly twice as frequently as parasitized birds ($\bar{x} = 4.70$ vocalizations min^{-1} unparasitized vs. $\bar{x} = 2.75$ vocalizations min^{-1} parasitized; Sharp and Kus 2006). The Least Bell's Vireo is a common host of the Brown-headed Cowbird (*Molothrus ater*); in some areas, as many as 80% of vireo nests are parasitized by cowbirds (U.S. Fish and Wildlife Service 1998). Brood parasitism is particularly costly for Bell's Vireos because parasitized

pairs rarely fledge any offspring (Kus 1999). Cowbird parasitism has contributed to local extirpations and dramatic declines of Least Bell's Vireo populations, resulting in the subspecies being listed as endangered by the U.S. Fish and Wildlife Service (1998). Moreover, Bell's Vireos vocalize frequently; males share incubation duties with females and often sing while sitting on the nest. The negative association between vocalization rate and probability of parasitism in the Least Bell's Vireo appears puzzling because it represents the pattern opposite of that reported in other species. However, the difference reported by Sharp and Kus (2006) was not statistically significant, leading them to suggest that "the differences could simply be due to random chance." Was the contradictory pattern reported by Sharp and Kus (2006) an anomaly, or does it reflect a pattern universal in all populations of Bell's Vireo? If the differences are real and Bell's Vireos somehow avoid the trade-off between vocalization rate and brood parasitism (and thereby prevent even higher rates of parasitism), why don't other species do the same?

To evaluate the ubiquity of the contradictory pattern in the Least Bell's Vireo, we sought to further evaluate the host-activity hypothesis by examining the relationship between vocal behavior and cowbird parasitism in another subspecies of Bell's Vireo, *V. b. arizonae*. In interpreting the relationship between host vocalization rate and brood parasitism, it is important to consider that the frequency of most songbirds' vocalizing changes through the breeding season (Howes-Jones 1985, Gottlander 1987, Avilés et al. 2009). Cowbirds are believed to locate host nests during the building stage (Friedmann 1929, Hann 1941) but parasitize nests during the egg-laying and early incubation stages (Friedmann 1929, Lowther 1993). Hence, a high vocalization rate during any of these three stages could increase the risk of brood parasitism, but the effect may be more pronounced at different stages. Additionally, fundamental causal pathways between vocalization rate and brood parasitism remain unexplored. Previous studies (Clotfelter 1998, Banks and Martin 2001, Svagelj et al. 2009) have assumed that avian brood parasites eavesdrop on vocalizing birds to locate and parasitize their nests. That is, cowbirds exploit the public information provided by their hosts and use this information to the host's detriment. Under this scenario, the positive correlation between vocalization rate and brood parasitism observed in past studies is caused by vocalization rate influencing the probability of parasitism. Accordingly, differences in vocalization rate between parasitized and unparasitized hosts should be expected before parasitism occurs, i.e., during the building and egg-laying stages. Alternatively, parasitized hosts may decrease their vocalization rate because of the parasite's effects on the host's behavior; for example, hosts could become "quieter" if they detect cowbirds near their nest (Uyehara and Narins 1995). Similarly, physiological constraints caused by nest parasitism could cause decreases in vocalization rates (e.g., parasitic eggs or nestlings could increase energetic demands on a host, leaving it with less energy for vocalizing). In the case

of this second causal pathway, a difference in vocalization rate between parasitized and unparasitized hosts should be expected after parasitism occurs, particularly during the incubation and nestling stages. This “chicken–egg” dilemma has not been considered in past tests of the host-activity hypothesis and has important evolutionary implications in the arms race between parasites and their hosts (Blanchet et al. 2009).

In this study, we tested a key assumption of the host-activity hypothesis with Bell’s Vireo: that vocalization rate is positively correlated with the incidence of brood parasitism. We explored the relationship between these two traits in greater detail by comparing vocalization rates between parasitized and unparasitized nests during all four stages of the nesting cycle. Elucidating relationships among parasitism, nesting stage, and vocalization rate not only clarifies the extent to which cowbirds use public information to locate nests of Bell’s Vireos but also facilitates formulation of mechanistic hypotheses to explain why some birds are parasitized while others are not.

METHODS

STUDY AREA

We studied populations of Bell’s Vireo breeding at three sites in southeastern Arizona in 2007: two sites at Cienega Creek Natural Preserve (32° 01′ N, 110° 38′ W) and one site at Posta Quemada Ranch (32° 03′ N, 110° 38′ W). Study sites consisted of riparian woodland with a canopy dominated by Fremont cottonwood (*Populus fremontii*), Goodding’s willow (*Salix gooddingii*), and mesquite (*Prosopis* spp.) and a shrub layer dominated by graythorn (*Ziziphus obtusifolia*). Sites were corridors of riparian woodland 1–1.5 km long and 13–99 m wide surrounded by Sonoran desert vegetation; they ranged from 1020 to 1050 m in elevation. Streams had ephemeral to intermittent flows and similar surface geology. Cowbirds and Bell’s Vireos have been sympatric in the region for approximately 150–200 years.

NEST SEARCHING AND MONITORING

At each site, we used parental behavior (Martin and Geupel 1993) to locate nests from April to July 2007. We monitored nests every 2 days until they failed or fledged young. During each visit, we noted whether the nest was parasitized or unparasitized and counted any parasitic eggs. We believe that we located >80% of nests because of the narrowness of habitat suitable for the vireo’s breeding (riparian woodland, surrounded by upland desert vegetation), the frequent nest searching by a large field crew, and the fact that Bell’s Vireo nests are relatively easy to locate.

AUDIO RECORDINGS

We attached a Radio Shack lapel microphone to a branch of the nest substrate 50–70 cm from the nest (modified from Clotfelter 1998) at a 45° angle above the nest with respect to a horizontal line outward from the nest. Microphones were connected to an Olympus digital voice recorder (model VN 2100PC or 3100PC) concealed in vegetation at least 1 m

from the nest. We recorded vireo vocalizations every 2 days between 06:00 and 13:00 during the nest-building (4–5 days), egg-laying (3–4 days), incubation (14 days), and nestling (10–12 days) periods (Kus et al. 2010). The number of recordings per nest varied from 1 to 14 because nests were located at different stages and some failed prior to fledging. In general, we used one recording per nest for each nesting stage in our analyses. For those nests with more than one recording for the same nesting stage, we took the mean vocalization rate of the multiple recordings. We did not make recordings on days with rain or when winds exceeded 5 km hr⁻¹. To reduce the risk of forced fledging, we ceased recording vocalizations at nests when vireo nestlings reached an age of 8 or 9 days. All activities had the approval of the University of Arizona’s Institutional Animal Care and Use Committee (no. 7673).

TRANSCRIPTIONS OF AUDIO RECORDINGS

We quantified vocalization rates by transcribing 30 min of each audio recording. We played recordings on a laptop computer through a set of Sony SRS-A27 speakers placed at a distance of 28 cm from the transcriber. We recorded all vireo vocalizations: primary songs (described phonetically as “cheedle-cheedle-cheedle-chee” or “cheedle-cheedle-cheedle-chew”; Brown 1993), incomplete songs, squeaky songs (also called courtship song), and calls. We included all vocalizations in our analysis (89% of transcribed vocalizations were songs) because we reasoned that cowbirds could cue in on any vocalization given by vireos near the nest. Moreover, several previous tests of the host-activity hypothesis (Uyehara and Narins 1995, Banks and Martin 2001) also included all vocalizations. One of us (SES) ranked the loudness of vireo vocalizations by ear, on a 7-point scale (1 = quietest and 7 = loudest). We assumed that loud vocalizations were generally those given nearest to the nest, whereas quiet vocalizations were those given farther from the nest. On the basis of behavioral observations, males did not appear to vocalize more softly when on or near the nest (Steckler 2009). To help account for songs sung by males other than the one at the nest, we attributed a primary song to a nonfocal vireo if either (1) two songs overlapped or one immediately followed another (i.e., no pause between two songs) and the two differed by any sound level, or (2) one song followed another by 2–10 sec and differed by at least two sound levels. In these cases, we assigned the louder song to the focal male and disregarded the other, under the assumption that he was closer to his nest than was a neighboring male.

STATISTICAL ANALYSES

We used an information-theoretic (AIC_c) approach to analyze our data. Information-theoretic methods allow analysts to evaluate strength of evidence of a given set of a priori hypotheses (Anderson et al. 2000). We chose not to use null-hypothesis testing because it has been criticized as uninformative (i.e., arbitrary *P*-values are used to judge the validity of relationships; Johnson

1999, Anderson et al. 2000). In contrast, AIC ranks a set of candidate models that are of explicit interest at the outset of the study and assigns a relative probability to each model (i.e., Akaike weight, w_i ; Anderson 2008). This offers a powerful approach to data analysis based on testing of alternative hypotheses (Chamberlin 1965) and is best suited for situations (such as ours) where the goal was to evaluate the validity of an explicit hypothesis against one or more alternative models. We used AIC to analyze (1) all of our data ($n = 51$ nests) and (2) a subset of our data that included only nests ($n = 8$ of the 51) at which we recorded vocalization rates during all four nesting stages. For the first analysis, we evaluated five general linear models to explain variation in vocalization rate: (1) a null (intercept-only) model, (2) a model with nesting stage only, (3) a model with parasitism status (nest parasitized or unparasitized) only, (4) a model with nesting stage and parasitism status, and (5) a global model that included nesting stage, parasitism status, and their two-way interaction. For the second analysis, we ranked the same set of five candidate models but used a repeated-measures general linear model with nesting stage as the repeated measure. We then repeated both of these analyses after excluding the softest vocalizations (i.e., the two lowest vocalization levels, which accounted for >60% of the total) because we were concerned that our microphones may have recorded vocalizations of neighboring (nonfocal) males. Because vocalization rate was the response variable in all of our models, our analyses implicitly assumed that parasitism influences vocalization rate. Deciding whether parasitism or vocalization rate is the appropriate response variable is arbitrary, however, because the causal pathway could be in either direction depending on the mechanism responsible for the association between the two traits (see above). Our goal was to compare vocalization rates of parasitized and unparasitized nests (see Banks and Martin 2001). We considered models with ΔAIC_c values >4 to have little support (Anderson 2008). We used SPSS 17.0 for all analyses (SPSS Inc., Chicago) and present all effect sizes as means \pm 1 SE.

RESULTS

Cowbirds parasitized nearly one third of vireo nests at the three study sites (28% of 98 nests). Unparasitized vireos vocalized more frequently than parasitized vireos, and differences were not consistent by nesting stage (Fig. 1). When all vocalizations were analyzed, unparasitized vireos vocalized nearly twice as often as parasitized vireos during building and incubation ($\bar{x} = 7.10 \pm 1.43$ vocalizations min^{-1} unparasitized vs. 4.81 ± 0.93 vocalizations min^{-1} parasitized for building; $\bar{x} = 5.22 \pm 0.64$ vocalizations min^{-1} unparasitized vs. 3.13 ± 0.67 vocalizations min^{-1} parasitized for incubation). The top model in the AIC analysis included nesting stage and parasitism status as predictors of total vocalization rate (Akaike weight = 50%; Table 1). Nesting stage and parasitism status were included in the top three AIC models, which together had 96% support as the most likely models. We found similar

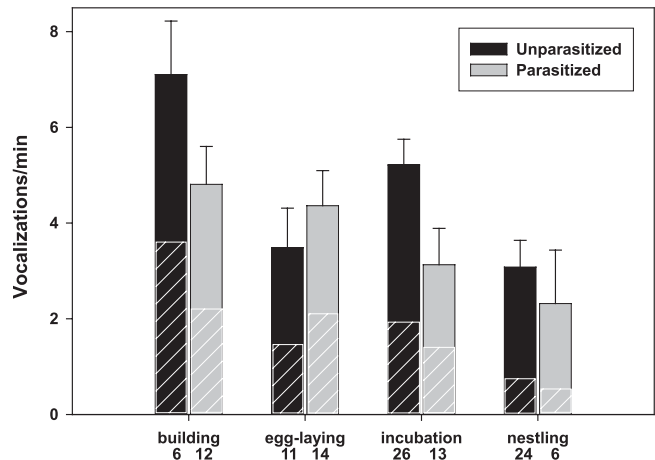


FIGURE 1. Rates of loud and of all vocalizations at unparasitized and parasitized nests of Bell's Vireos breeding at three sites in southeastern Arizona, 2007. Bars represent means \pm SE during four stages of nesting. Hatched areas indicate loud vocalizations only. Numbers of nests are shown beneath bars.

results when we examined only loud vocalizations for all nests ($\bar{x} = 3.55 \pm 1.12$ vocalizations min^{-1} unparasitized vs. 2.17 ± 0.56 vocalizations min^{-1} parasitized for building; $\bar{x} = 1.96 \pm 0.47$ vocalizations min^{-1} unparasitized vs. 1.45 ± 0.39 vocalizations min^{-1} parasitized for incubation; Fig. 1).

The relationship between parasitism status and vocalization rate also differed among nesting stages when we analyzed the subset of 8 nests at which we measured vocalization rates during all four stages. Unparasitized vireos vocalized nearly three times as often as parasitized vireos during the building stage ($\bar{x} = 7.03 \pm 2.25$ vocalizations min^{-1} unparasitized vs. 2.57 ± 0.80 vocalizations min^{-1} parasitized) and more than four times as often during incubation ($\bar{x} = 8.39 \pm 0.94$ vocalizations min^{-1} unparasitized vs. 1.95 ± 1.04 vocalizations min^{-1} parasitized; Fig. 2). The top AIC model (and only model

TABLE 1. Generalized linear models explaining effects of nesting stage and Brown-headed Cowbird parasitism on total and loud vocalization rates for all nests ($n = 51$) of Bell's Vireos breeding at three sites in southeastern Arizona, 2007. GLM results for rates of loud vocalizations are in parentheses. Models are listed in order of decreasing support.

Explanatory variables ^a	K^b	ΔAIC_c^c	w_i
STAGE, PAR	3	0.0 (1.5)	0.496 (0.294)
STAGE	2	1.5 (0.0)	0.237 (0.630)
STAGE, PAR, STAGE \times PAR	4	1.5 (4.6)	0.230 (0.064)
None	1	6.0 (8.5)	0.024 (0.009)
PAR	2	7.4 (10.5)	0.012 (0.003)

^aSTAGE = nesting stage (building, egg-laying, incubation, or nestling), PAR = parasitism status (parasitized or unparasitized).

^bNumber of parameters.

^cLowest $AIC_c = 553.4$ (446.8).

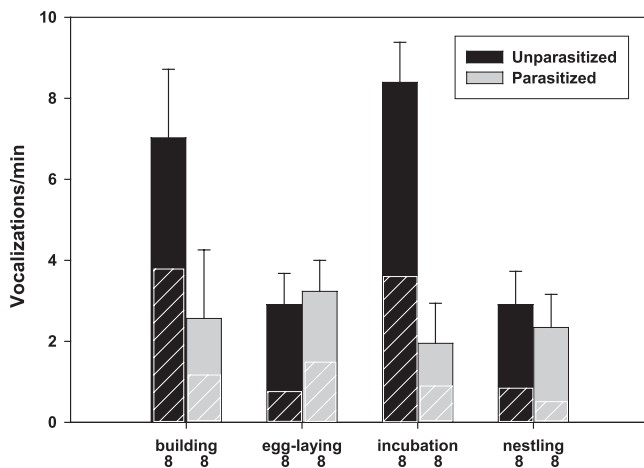


FIGURE 2. Rates of loud and of all vocalizations at unparasitized and parasitized nests of Bell's Vireos breeding at three sites in southeastern Arizona, 2007. Each nest ($n = 8$) was measured during all four stages of nesting. Bars represent means \pm SE. Hatched areas indicate loud vocalizations only. Numbers of nests are shown beneath bars.

with $\Delta AIC_c \leq 4$) was the global model, with nearly 100% support ($w_i = 0.99$; Table 2). Again, the pattern was similar when we restricted our analysis to include only loud vocalizations ($\bar{x} = 3.74 \pm 1.76$ vocalizations min^{-1} unparasitized vs. 1.15 ± 0.69 vocalizations min^{-1} parasitized for building; $\bar{x} = 3.61 \pm 1.80$ vocalizations min^{-1} unparasitized vs. 0.93 ± 0.62 vocalizations min^{-1} parasitized for incubation; Fig. 2); the global AIC model was the top model and had 97% support (Table 2).

DISCUSSION

Our study failed to support the host-activity hypothesis; vocalization rate was negatively, not positively, correlated with cowbird parasitism of Bell's Vireos. However, the difference

TABLE 2. Generalized linear models explaining effects of nesting stage and Brown-headed Cowbird parasitism on total and loud vocalization rates for a subset of Bell's Vireo nests ($n = 8$) that were measured during all four stages of nesting. GLM results for rates of loud vocalizations are in parentheses. Models are listed in order of decreasing support.

Explanatory variables ^a	K	ΔAIC_c^b	w_i
STAGE, PAR, STAGE \times PAR	4	0.0 (0.0)	0.99996 (0.971)
STAGE, PAR	3	21.2 (7.4)	0.00002 (0.024)
STAGE	3	22.2 (10.9)	0.00002 (0.004)
PAR	3	29.2 (14.0)	0.0000005 (0.001)
None	2	30.4 (19.2)	0.0000003 (0.00007)

^aSTAGE = nesting stage (building, egg-laying, incubation, or nestling), PAR = parasitism status (parasitized or unparasitized).

^bLowest $AIC_c = 137.8$ (115.5).

in vocalization rate between unparasitized and parasitized vireos was clearest during only two of the four stages of nesting. The pattern was most pronounced for nests in which we were able to control for intraspecific variation in vocalization rate (using a repeated-measures model). Parasitized vireos tended to vocalize infrequently at all stages. Our results corroborate those of Sharp and Kus (2006) and demonstrate that their unusual result was not an anomaly. These patterns in two subspecies of Bell's Vireo contradict the positive relationship between vocalization rate and brood parasitism reported in other cowbird hosts (Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001, Garamszegi and Avilés 2005). Our findings, together with those of Sharp and Kus (2006), demonstrate that the relationship between host activity and cowbird parasitism is not consistent across all host species and varies by nesting stage within a species. Our study highlights the importance of (1) including nesting stage and (2) controlling for individual variation in vocalization rate in future tests of the host-activity hypothesis and in efforts to explain the cause of the negative correlation between vocalization rate and parasitism in Bell's Vireo.

Our study examined the relationship between all host vocalizations and the risk of cowbird parasitism. However, different vocalization types may relate to parasitism risk differently; these relationships could also differ by host species. Previous investigations varied in the type of vocalizations analyzed. Some examined all vocalizations including calls and songs (Uyehara and Narins 1995, Banks and Martin 2001, Sharp and Kus 2006, this study), some examined subsets of male and female vocalizations (Clotfelter 1998), and some examined songs only (Garamszegi and Avilés 2005, Avilés et al. 2009). Future studies should examine all vocalization types (but each one separately) to further clarify relationships between host vocal behavior and the probability of cowbird parasitism. Using sonograms to distinguish individuals by acoustic structure would be a particularly useful approach for analyzing audio recordings of cowbird hosts. We did not observe differences in loudness in male vireos' vocalizations on vs. off the nest. Nonetheless, future work should test this assumption by comparing audio recordings to behavioral observations of vireos at the nest. Many factors may influence song rate (e.g., age, breeding status, time in the breeding season), and these should be considered in analyses.

Although nests are vulnerable to cowbird parasitism from building to as late as the middle of incubation (Friedmann 1929, Lowther 1993), temporal variation in vocalization rate is common in birds and reinforces the importance of accounting for nesting stage in examination of relationships between vocalization rate and brood parasitism. Previous studies varied greatly in terms of when they measured hosts' vocalization rate: before nesting began (Avilés et al. 2009), during only one nesting stage (Clotfelter 1998, Banks and Martin 2001), or during several nesting stages (Uyehara and Narins 1995,

Garamszegi and Avilés 2005, Sharp and Kus 2006). Pooling data across nesting stages for analyses intended to examine the relationship between vocalization rate and brood parasitism may obscure the biological significance of how vocalization rate influences parasitism risk or, conversely, of how the act of parasitism affects vocalization rate. The difference in vocalization rate by nesting stage we observed in Bell's Vireo is compatible with the idea that vocalizing serves different functions at different stages of the nesting cycle. For example, high rates of vocalization during nest building may help males guard females and stimulate them to breed, whereas high rates during incubation may help males coordinate nest exchanges with females (Howes-Jones 1985).

Why doesn't frequent vocalizing increase the risk of parasitism for Bell's Vireos? One potential explanation is that host density and parasitism risk are negatively correlated (Fretwell 1977, Zimmerman 1983, Spautz 1999, Carello and Snyder 2000; but see Jensen and Cully 2005). Such a relationship could explain the patterns we observed between our measure of vocalization rate and brood parasitism if focal birds sing more frequently or if our recordings included more vocalizations of nonfocal birds in areas of higher densities of vireos. This *host-density* hypothesis assumes that host density and parasitism risk are negatively correlated. At least one study (Barber and Martin 1997) found a positive (rather than negative) relationship between host density and incidence of brood parasitism. Given the relatively low densities of Bell's Vireo at our study sites (average of 1.5 birds detected per point on unlimited-radius point-count surveys; C. J. Conway, unpubl. data) and the large number of eggs that female cowbirds are capable of laying over the breeding season (as many as 41 eggs; Scott and Ankney 1980), we do not believe this hypothesis explains the negative association between vocalization rate and probability of brood parasitism that we observed. However, the host-density hypothesis needs to be considered because the methods typically used to record host vocalization rate often include some unknown portion of songs and calls from nonfocal birds.

Sharp and Kus (2006) suggested that the nests of unparasitized vireos may have been concealed by more vegetation, reducing the probability of cowbirds discovering them and allowing the vireos to vocalize more frequently. Sharp and Kus found percent nest concealment to be an important predictor of parasitism, which supports this *nest-concealment* hypothesis. The nest-concealment hypothesis predicts that (1) vocalization rate and nest concealment should be positively correlated and (2) the probability of brood parasitism and nest concealment should be negatively correlated. The nest-concealment hypothesis was the only potential explanation discussed by Sharp and Kus (2006), but there are many hypotheses that can potentially explain the pattern observed in Bell's Vireo (Steckler 2009). A third explanation is that frequent vocalizing may reflect coordination between mated

pairs to help prevent cowbirds from accessing nests. This *mate-communication* hypothesis proposes that efficient nest exchanges reduce the amount of time a nest is left unattended for a female cowbird to parasitize and that cowbirds are less likely to parasitize a nest with an adult present. A high rate of vocalization may better coordinate nest exchanges between mates during incubation, as males contribute to incubation duties and often vocalize when approaching or departing the nest (Brown 1993). Hence, the mate-communication hypothesis predicts that (1) nest attentiveness should be positively correlated with vocalization rate and (2) the probability of parasitism should be negatively correlated with nest attentiveness. A fourth alternative proposes that if frequent vocalizing by vireos attracts nest predators, cowbirds may avoid parasitizing nests of birds vocalizing at high rates. This *predator-attraction* hypothesis (Avilés et al. 2006) assumes that the vireo's primary nest predators use aural cues to locate nests, and that cowbirds base parental-investment decisions on perceived predation risk. Indeed, in a comparative analysis across species, Avilés et al. (2006) found that the frequency of brood parasitism and rate of nest predation were negatively correlated. This hypothesis predicts that (1) vireos whose nests are eventually depredated should vocalize at rates higher than do those whose nests are eventually successful and (2) the probability of brood parasitism should be negatively correlated with probability of nest predation.

Conversely, the causal pathway may be in the other direction, parasitism altering vocalization rate (not vice versa), and this could explain why unparasitized vireos vocalize more. At least two potential hypotheses assume this alternative causal pathway. The *energy-allocation* hypothesis proposes that the addition of a cowbird egg to a vireo clutch increases total clutch mass, forcing incubating males to allocate more energy toward incubation at the expense of vocalizing. For small passerines, even moderate increases in clutch mass can increase daily energy expenditure during incubation (Coleman and Whittall 1988, Moreno and Carlson 1989). The energy-allocation hypothesis predicts that (1) vocalization rate should be negatively correlated with clutch mass and (2) vocalization rate should decrease after parasitism. Alternatively, vireos may be able to assess relative parasitism risk via cowbird density around nests (Forsman and Martin 2007). This *parasite-assessment* hypothesis proposes that hosts adjust vocalization rate on the basis of perceived parasitism risk, so that individuals nesting in areas of low cowbird densities vocalize more frequently. Individuals forced to settle in lower-quality areas (those with higher cowbird densities) may be forced to reduce their vocalization rate. The parasite-assessment hypothesis predicts that hosts' vocalization rate should be negatively correlated with local cowbird density.

Future studies should test explicit predictions of these (and other) alternative hypotheses to help determine the underlying reason why vocalization rate and probability of

parasitism are negatively, rather than positively, correlated in Bell's Vireo. Comparative analyses may be particularly informative if a negative relationship between vocalization rate and probability of brood parasitism is found in other species. Twelve of North America's 13 vireo species vocalize while on the nest (Leonard 2008); future studies should target these species to determine whether the pattern between vocalization rate and probability of parasitism is the same for them as for Bell's Vireo. Moreover, additional information on exactly how cowbirds locate nests will help illuminate the potential trade-off between vocalization rate and brood parasitism. Conspicuous behavior near the nest may increase probability of brood parasitism for some, but not all, species. Future studies that examine the relationship between vocalization rate and probability of parasitism in other species will provide a deeper understanding not only of factors influencing cowbird parasitism but also of other functions of avian vocal behavior and the ground rules underlying the evolutionary arms race between brood parasites and their hosts.

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