TWO SUBSPECIES OF WARBLING VIREO DIFFER IN THEIR RESPONSES TO COWBIRD EGGS

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ABSTRACT: Using real cowbird eggs, we experimentally parasitized 41 nests of the Warbling Vireo (*Vireo gilvus*), three each in British Columbia and Colorado, five in Montana, and 30 in Manitoba, and recorded whether the cowbird eggs were accepted or rejected. Cowbird eggs were accepted at all nests tested in British Columbia and Colorado, but both acceptance and rejection were recorded in Montana. In Manitoba, all cowbird eggs were rejected (29 by puncture-ejection, one by desertion). The results suggest acceptance by a western subspecies of the Warbling Vireo, *V. g. swainsonii*, and rejection by the eastern subspecies, *V. g. gilvus*. The geographic variability in acceptance/rejection agrees with suggested taxonomic differences for the Warbling Vireo, i.e., that there are two species and that neither appears to vary in response to the presence of cowbird eggs in its nests.

Species of birds that suffer reduced reproductive success when parasitized by Brown-headed Cowbirds (*Molothrus ater*) should evolve strategies that reduce or eliminate the costs of parasitism, especially because cowbird eggs are distinguishable from the eggs of most host species. Adaptations for rejection of parasitic eggs from nests have evolved in some species, but most species accept cowbird eggs (Rothstein 1975, 1990). Why only a few species reject cowbird eggs has been attributed to the duration of exposure to the selective pressure of cowbird parasitism (Rothstein 1975) or constraints on the ability of small hosts to eject cowbird eggs from the nest (Rohwer and Spaw 1988). Among the ejecter species, the larger ones grasp and remove cowbird eggs with their bills, whereas the smaller species puncture-eject them (Rohwer and Spaw 1988).

Recently, Sealy (1996) determined experimentally that the Warbling Vireo (*Vireo gilvus*) removes cowbird eggs from its nests. At 15 g, it is the smallest species in North America known to do so (Sealy 1996). This species' responses to cowbird eggs also appear to vary across its geographic range. A literature survey of the frequency of parasitism in various populations of Warbling Vireos (table 2 of Sealy 1996) revealed that 0 to 11% of Warbling Vireo nests were parasitized in populations within and east of the Central Great Plains, whereas 50 to 70% of nests were parasitized in populations west of the Great Plains. Where experimental data are lacking, Friedmann et al. (1977) assumed that a species accepts cowbird eggs (i. e., is an accepter) if 20% or more of its nests are recorded parasitized. Under this definition, western populations of the Warbling Vireo would be classified as accepters, whereas central and eastern populations reject parasitism. Sealy's (1996) experiments on Warbling Vireos in Manitoba support the assessment of birds there as rejecters.

From those data, Sealy (1996) concluded that the apparent geographic variation in response to parasitism by Warbling Vireos generally fits with data regarding the duration of sympatry with cowbirds by eastern versus western populations (Mayfield 1965, Rothstein 1994, but see Ward and Smith 1998). Experiments on populations across the breeding range of the Warbling Vireo are required to confirm the extent of responses to cowbird eggs. Here we present the results of tests on nests of the Warbling Vireo in British Columbia, Colorado, Montana, and Monitoba.

METHODS

We experimentally parasitized Warbling Vireo nests at four localities, described by Ward and Smith (2000), Marvil and Cruz (1989), MacKenzie et al. (1982), and Tewksbury et al. (1998). British Columbia: In 1994, David Ward parasitized one nest about 7 km WNW of Oliver (49° 10′ N, 119° 13′ W) and two nests 7 km E of Okanagan Falls (49° 21′ N, 119° 33′ W), in the southern Okanagan Valley. Montana: Banks tested five nests in 1996, two along the Bitterroot River (45° 56′ N, 114° 08′ W and 46° 07′ N, 114° 10′ W), three along Rock and Lick creeks (45° 09′ N, 114° 13′ W) and McCoy Creek (45° 59′ N, 114° 12′ W). One of these nests was naturally parasitized, receiving one cowbird egg. Colorado: In 1994, Chace tested two nests and recorded the response to a naturally laid cowbird egg in another nest, all in Boulder County. One nest was near Ward on the Sawtooth Springs Ranch (40° 07′ N, 105° 28′ W), the others were on Flagstaff Mountain (40° 00′ N, 105° 18′ W). Manitoba: Sealy (1996) parasitized 16 nests and recorded the response to natural parasitism at one nest in 1992 and 1993 at Delta Marsh (50° 11′ N, 98° 19′ W). He tested 13 additional nests in 1996 and 1997, for a total of 30 nests at this site.

We introduced one real cowbird egg into each nest during the laying stage or incubation stage. In all but one nest, cowbird eggs were added before 12:00 (respective standard times). A host egg was not removed from nests because egg removal by cowbirds is variable (Sealy 1992). Most nests were inspected the day after parasitism and every day after that until the cowbird egg disappeared or had remained in the nest for at least 5 days, when it was assumed to be accepted (Rothstein 1975, Sealy 1996). We watched all nests tested in Colorado and Montana and 17 nests in Manitoba for 30 to 60 min immediately following parasitism to record reactions of adults to the parasitized clutches (see Sealy 1996 for descriptions of behavioral responses to experimental parasitism in Manitoba).

RESULTS

Cowbird eggs were accepted at all nests tested in British Columbia ($n = 3$, D. Ward, pers. comm.) and in Colorado ($n = 3$). One of these nests was naturally parasitized, receiving one cowbird egg. In Montana, cowbird eggs were accepted at three nests (one experimentally parasitized during laying; two during incubation, one clutch already parasitized) and ejected from two incubated clutches.

Reactions of females upon their return to the parasitized nests differed. In Manitoba, at 16 nests where an adult returned to the nest during the observation, the vireo punctured or broke the cowbird egg and ejected it, generally within seconds of its return to the nest (description of behavior in Sealy 1996). At the three Colorado nests, vireos returned unagitated and settled on their eggs without probing or pecking the cowbird egg or behaving in any other way that suggested recognition of the foreign egg. Vireos also resumed incubation at the five Montana nests with no signs of recognition of the cowbird eggs, although the cowbird eggs were later ejected at two nests.

DISCUSSION

Warbling Vireos' responses at experimentally parasitized nests varied. Cowbird eggs were accepted at all nests tested in British Columbia and Colorado but were rejected from all nests tested in Manitoba. In Montana, cowbird eggs were accepted at three and ejected from two nests. Collectively, these results are subject to two interpretations. The first is that acceptance and rejection behavior in the Warbling Vireo is variable and that therefore this species joins a small group of species in which acceptance or rejection is not near 100%, such as the Yellow-breasted Chat (*Icteria virens*, Burhans and Freeman 1997), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*, Dufty 1994), and Common Grackle (*Quiscalus quiscula*, Peer and Bollinger 1997). The other interpretation is that despite the variable responses to parasitism, Warbling Vireos do not conflict with the generalization of low variation in responses because the Warbling Vireo as traditionally constituted is actually two sibling species (Johnson et al. 1988, Sibley and Monroe 1990, Murray et al. 1994).

Sibley and Monroe (1990) recognized two species of Warbling Vireo, *Vireo gilvus* (Eastern Warbling-Vireo) and *V. swainsonii* (Western Warbling-Vireo). The species differ in morphology and vocalizations (J. C. Barlow in Sibley and Monroe 1990) and by about 3% sequence divergence in their mitochondrial DNA (Murray et al. 1994). At one point where their ranges meet, in north-central Alberta, males singing the *gilvus* song-type and males singing the *swainsonii* song-type have been found on adjacent territories, but interbreeding between the two has not been recorded (W. B. McGillivray and J. C. Barlow pers. comm.). Although the limits of the ranges of the eastern and western subspecies of the Warbling Vireo are known only roughly (e.g. Sibley 1940, Worthen 1969, Browning 1974, Voelker and Rohwer 1998), we suspect the two subspecies, or species, meet also in western Montana (see maps in Voelker and Rohwer 1998) because both acceptance and rejection of cowbird eggs were recorded there. Confirmation of the trend toward acceptance of cowbird eggs in a western subspecies and rejection by the eastern one, suggested by our limited data, requires more testing of nests across the entire range of the Warbling Vireo, especially of birds farther east and preferably with the attendant species or subspecies verified at each nest.

The variable response to parasitism supports the contention of two species of Warbling Vireo, with *swainsonii* occurring from the Rocky Mountains to the Pacific Ocean and *gilvus* from the Rockies to northeastern

North America. As cowbirds were found historically from the Rockies to the eastern slopes of the Sierra Nevada and Cascade Range (Rothstein 1994), *swainsonii* is likely to have experienced some parasitism before the cowbird's range extensions since 1900. But the critical thing in *gilvus* being a rejecter is that it likely experienced extensive parasitism in and adjacent to the Great Plains. Sealy (1996) assumed that *swainsonii*, though smaller than *gilvus* (Ridgway 1904), is large enough not to be physically constrained from ejecting cowbird eggs. If not, and rejection is more costly, these individuals may be in equilibrium with cowbird parasitism. This seems unlikely, however, because the usual result of parasitism on Warbling Vireos is the loss of their entire brood (references in Sealy 1996). Therefore, there may be essentially no cost to rejection, only a reduction in the net value of not rejecting cowbird eggs.

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