EVOLUTION OF HOST DEFENSES AGAINST BROOD PARASITISM: IMPLICATIONS OF PUNCTURE-EJECTION BY A SMALL PASSERINE

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ABSTRACT.—In Manitoba, Warbling Vireos (*Vireo gilvus*) rejected eggs of the Brown-headed Cowbird (*Molothrus ater*) from 1 naturally parasitized nest and 16 experimentally parasitized nests studied in 1992 and 1993. Vireos rejected single, real cowbird eggs in 16 cases by ejection and 1 by desertion. Observations at nests during the first hour after parasitism showed that: (1) females carried out four ejections, whereas two of three unsuccessful ejection attempts were by males; and (2) the four observed egg removals were by puncture-ejection (entire cowbird egg removed or pieces of shell removed after egg contents consumed). These are the first observations of puncture-ejection by the Warbling Vireo, which is now the smallest species (15 g) known to eject cowbird eggs in this manner. Two competing hypotheses, evolutionary lag and evolutionary equilibrium, have been advanced to explain acceptance of brood parasitism by hosts parasitized with nonmimetic eggs. One prediction of the equilibrium hypothesis, that small hosts incur greater costs than large hosts when ejecting eggs, was examined by comparing the costs of rejection at experimentally parasitized nests of Warbling Vireos and larger Northern Orioles (*Icterus galbula*, 33 g). Warbling Vireos lost or damaged 5 of their own eggs while rejecting the 17 cowbird eggs, or 0.29 vireo eggs for every cowbird egg rejected. The cost to Northern Orioles of this behavior was 0.38 oriole eggs per cowbird egg ejected, which was not significantly different from the cost incurred by Warbling Vireos. My results by default support the evolutionary-lag hypothesis because the smaller species did not incur greater costs during puncture-ejection than the larger species. Warbling Vireos in and east of the Great Plains, *V. g. gilvus*, reject cowbird eggs, whereas individuals in a population west of the Great Plains, *V. g. swainsonii* (12 g), apparently accept the eggs. The different responses to cowbird eggs possibly reflect differences between two sibling species that have been in contact with cowbirds for different lengths of time, assuming that individuals in the western population are not below the minimum value for size of an ejecter. *Received 16 August 1994, accepted 27 January 1995.*

MOST HOSTS THAT ACCEPT the eggs or nestlings of parasitic Brown-headed Cowbirds (*Molothrus ater*) appear to behave nonoptimally (Rothstein 1982) because this parasitism often lowers their reproductive output (Friedmann 1963, Rothstein 1975a, Payne 1977, May and Robinson 1985). Thus, hosts should be expected to evolve antiparasite strategies, especially because cowbird eggs are distinguishable from the eggs of most host species. Although highly effective nest defense would eliminate the need for egg recognition, many nests of some aggressive hosts are still parasitized (Neudorf and Sealy 1992, 1994). Thus, it is puzzling that most hosts accept cowbird eggs when effective adaptations for the rejection of parasitic eggs have been evolved by some species, often in the same evolutionary lineages (Hamilton and Orians 1965, Rothstein 1975a, 1982, 1990, Rich and Rothstein 1985, Ortega and Cruz 1988).

Evolutionary lag versus equilibrium are two general views that have been proposed to explain acceptance by many hosts parasitized with nonmimetic eggs (Rothstein 1990). Under the evolutionary-lag hypothesis, rejection would be adaptive, but has not yet become common or even detectable because it takes time for new genetic variants to appear and increase as a result of selection (Mayfield 1965, Rothstein 1975a, 1982, Davies and Brooke 1988). Once the rejection behavior appears in a species, it will be fixed rapidly (Rothstein 1982). No physical constraints are assumed here because large hosts can remove cowbird eggs by grasping them in their bills, and small hosts can puncture or break the eggs and then remove them or desert their

nests and lay a new clutch in a new nest (Rothstein 1975a).

Under the equilibrium view, the costs of rejection are greater than acceptance and, therefore, rejection is less adaptive (Zahavi 1979, Rohwer and Spaw 1988). One equilbrium hypothesis, the "puncture-resistence" hypothesis, assumes that small birds cannot grasp cowbird eggs to remove them from their nests, but instead must first pierce them (Spaw and Rohwer 1987, Rohwer and Spaw 1988). However, ejection by spiking or breaking cowbird eggs would be disadvantageous if it led to accidental breakage or soiling of host eggs (Rothstein 1975a). Rohwer and Spaw (1988) argued that the thick shells of cowbird eggs render the cost of ejection for a small host greater than the cost of rearing a cowbird (see also Røskaft et al. 1993), assuming that puncture-ejection would be a readily evolved alternative (but see Rothstein 1982). The puncture-resistance hypothesis predicts that ejection costs will rise as host size decreases, with small hosts being better off rearing the cowbird than attempting to eject the thick-shelled cowbird egg. Small hosts, therefore, should not evolve puncture-ejection. Regardless of size or other attributes, nest desertion should always be a rejection option for parasitized individuals.

In 1986, I recorded anecdotal evidence that Warbling Vireos (*Vireo gilvus*) reject cowbird eggs. A cowbird egg observed in a vireo's nest was found the next day on the ground under the nest, punctured. Weighing only 15 g (Dunning 1993), Warbling Vireos would be the smallest species known to eject cowbird eggs (see Rohwer and Spaw 1988). If the relationship between host size and ejection cost is linear, the ability of Warbling Vireos to eject cowbird eggs would be support for the idea of evolutionary lag. Only a dozen other species are known to eject cowbird eggs (Rothstein 1976a, Rich and Rothstein 1985, Rohwer and Spaw 1988). The two smallest of these species, the Cedar Waxwing (*Bombycilla cedrorum*) and Northern Oriole (*Icterus galbula*), both weigh about 33 g and remove cowbird eggs by puncture-ejection (Rothstein 1976a, 1977, Rohwer et al. 1989). Larger species that eject cowbird eggs generally remove cowbird eggs by grasp-ejection (Rohwer and Spaw 1988).

My study has two objectives: (1) to confirm experimentally that Warbling Vireos reject cowbird eggs, and by what method; and (2) to test the hypothesis that, during ejection of a cowbird egg, small birds damage their own eggs more than do large birds. I used real cowbird eggs to parasitize clutches of the Warbling Vireo and the larger Northern Oriole.

METHODS

To determine the frequency of cowbird parasitism, I inspected unmanipulated Warbling Vireo nests from 1975 to 1986 and experimentally parasitized vireo nests in 1992 and 1993 in the forested dune ridge that separates Lake Manitoba and Delta Marsh, Manitoba (50°11'N, 98°19'W; habitat and nest sites described in MacKenzie et al. 1982). In 1992 and 1993, I experimentally parasitized 16 Warbling Vireo nests by introducing one fresh, genuine cowbird egg into each nest between 0700 and 0900 CST during laying (nine nests) and up to five days into the incubation period (seven nests). In addition, one nest was parasitized by a cowbird in 1993. At 13 experimental nests that I could reach by hand, I placed the cowbird egg carefully into the nest and checked to ensure that neither it nor any of the vireo eggs was damaged or broken. In addition, using a guyed extension ladder (Rohwer 1988), I parasitized three high nests (two containing one vireo egg when parasitized, one containing four eggs) by hoisting the cowbird egg in a padded camera-film container affixed to a pole, and tipped the egg into the nest from about 1 cm above the host's eggs. Using a mirror, I determined later that no eggs were broken or damaged (i.e. discolored) in any of these nests as a result of this procedure. I did not remove a vireo egg from the experimental nests because cowbirds do not always remove a host egg from nests they parasitize, and host-egg removal does not influence host acceptance (Davies and Brooke 1989, Sealy 1992, 1995).

I immediately initiated 1-h observation bouts at nests that were visible using a 20× telescope from a blind or hidden vantage point 15 to 20 m from the nest. I did not watch nest 93-2 (Table 1) because it was parasitized naturally earlier on the morning that I had intended to parasitize it. During the observation bouts, I recorded the vireos' responses to the cowbird egg. As only male Warbling Vireos sing (Roberts 1932:184, Sutton 1949, Howes-Jones 1985), I distinguished between males and females at most nests by identifying the singer. The males at two nests (93-7, 93-11) and the female at another (92-3) wore metal bands. If an introduced egg was ejected from a nest within the hour, I observed the nest for an additional 15 min. At the end of 1 h following parasitism, I inspected the three vireo nests that I could not watch and checked them again 4 h later, along with the other experimental nests that after 1 h still contained the cowbird egg. I inspected each nest every morning thereafter until the cowbird egg disappeared. I continued daily

TABLE 1. Warbling Vireo nests subjected to experiments simulating Brown-headed Cowbird parasitism.

Nest no.[a]	Clutch size[b]	No. eggs present when parasitized[b,c]	Nest stage when parasitized[a]	Type of rejection[a]	Hours for rejection[d]	Vireo eggs missing (M) or damaged (D)
92-1	4	4(A)	I	E	24	None
92-2	4	4(P)	I	E	24	None
92-3	4	4(P)	I	E	<1[c]	None
93-2[e]	4	2	L	E	24	1 M[f]
93-3	3	3(P)	L	E	5	None
93-4	≥4	4(A)	I	D	5	2 M
93-5	3	3(P)	I	E	<1	None
93-7	5	4(P)	L	E	48	None
93-8	≥4	2(P)	L	E	5	2 M, 1 D
93-9	4	4(P)	I	E	<1	None
93-11	4	1(A)	L	E	5	None
93-12	4	1(A)	L	E	96	2 M[g]
93-13	3	3(P)	I	E	24	None
93-14	≥2	1(A)	L	E	24	None
93-15	4	1(P)[h]	L	E	5	None
93-16	4	4(P)	I	E	5	None
93-17	4	4(P)	I	E	<1	None

[a] Prefixes of nest numbers equal year in which experiment conducted. All experimental eggs were real cowbird eggs. Symols: (I) incubation; (L) laying; (E) egg ejected; (D) nest contents deserted. All nests were parasitized between 17 and 29 June 1992, and 9 and 28 June 1993.

[b] Additional egg(s) could have been laid in nests where "≥" precedes clutch size. Uncertainties exist for different reasons (e.g. nest deserted on day of parasitism, which occurred on day the fourth egg was laid and, hence, at least one more egg could have been laid [93-4]; visits to nests ceased before it was certain that egg laying was completed [93-8, 93-14].

[c] Adult present (P) or absent (A) at nest when parasitized.

[d] Nests where "<" precedes number of hours indicates ejection occurred during the 1-h observation bout.

[e] Nest 93-2 parasitized by cowbird. Missing egg probably removed by the cowbird; thus, nest was not used in assessment of cost of ejection.

[f] Missing egg probably removed by a cowbird.

[g] Two vireo eggs tossed out of nest during severe wind on 23 June, two days after cowbird egg ejected.

[h] Although parasitism occurred on 23 June when nest contained one egg, one host egg had already disappeared.

to inspect all except two nests parasitized during laying to determine the final clutch size. Rothstein (1975a, b) regarded as "rejecter species" those that removed, damaged or buried eggs, or deserted the nests, within five days of the experimental introduction of cowbird eggs. He regarded species not showing any of these behaviors as "accepter species." To determine whether Warbling Vireos incurred a higher cost as a result of ejecting cowbird eggs than did a larger host species, the Northern Oriole, I parasitized 16 oriole nests using the same experimental protocol as above.

RESULTS

Natural parasitism on Warbling Vireos.—Parasitism was detected at 2 of 56 (3.6%) Warbling Vireo nests inspected on the study area. This sample included the 16 nests in which I introduced a cowbird egg in 1992 and 1993, and, hence, may be biased if cowbirds avoid already-parasitized nests (see Ortega et al. 1994). Parasitism was detected at 1 of 39 unmanipulated nests (2.6%) observed before 1992. The first case of parasitism was recorded on 2 June 1986, the morning the vireo laid its second egg. The next morning the nest contained three vireo eggs, but the cowbird egg was on the ground under the nest with a small hole in its shell. The next day the nest was empty and deserted.

The second nest (93-2) was parasitized on 9 June 1993, the day the vireo laid its third egg. At 0846 the nest contained three host eggs plus the cowbird egg, but by 1320 it contained only three vireo eggs, each unsoiled and undamaged. Beneath the nest was a piece of cowbird egg shell with a hole (maximum diameter, 3.2 mm). The cowbird probably parasitized the nest around 0400, prior to sunrise (see Neudorf and Sealy 1994), and this probably was followed within 1 h by the laying of the vireo's third egg (unpubl. data). Thus, the cowbird egg was ejected between 5 and 24 h after parasitism. At 0837 on 10 June, the nest still contained three vireo eggs, but the (marked) third-laid vireo egg was gone, indicating a fourth egg had been laid (determined later to be the final egg of the clutch). Three vireos fledged from this nest.

Responses to experimental parasitism.—Warbling Vireos rejected the cowbird egg at all 16 experimentally parasitized nests and at the single nest parasitized by a cowbird in 1993. Rejection was by ejection at 16 nests (15 experimental nests, 1 naturally parasitized nest) and desertion at 1 nest (Table 1). Rejection occurred at all nests, whether parasitized during laying or incubation, and regardless of whether a vireo was flushed from the nest at the time of parasitism (Table 1). However, not all Warbling Vireos rejected cowbird eggs as soon as they returned to their nests after the experimental parasitism. Of the 16 ejections (Table 1), vireos removed cowbird eggs within 1 h from four nests (25%), 5 h from five nests (31.3%), 24 h from five nests (31.3%), 48 h from one nest (6.3%), and 96 h from one nest (6.3%). Although sample sizes were small, there was no significant difference in the time to ejection (i.e. 24 h vs. >24 h) of cowbird eggs introduced into nests at the laying or incubation stage (Fisher exact test, df = 1, $P > 0.99$).

One experimentally parasitized nest (93-4) was deserted after two vireo eggs had been removed (probably by the vireos). The behavior of the adults at this nest during the 1-h observation bout is described in the Appendix. Females ejected the cowbird eggs from four nests (92-3, 93-5, 93-9, 93-17) within the first hour after parasitism (Table 1). From these nests, vireos removed three cowbird eggs by spiking them with closed bills and carrying them impaled on their bills more than 5 m from the nest. At the fourth nest (93-5), the vireo broke the cowbird egg into at least two pieces, consumed some of egg's contents, and then carried away each piece separately; one piece was moved about 5 m away and the other 8 m (details of observed ejections in the Appendix). Males at two nests (93-3, 93-11) and the female at a third nest (93-7) attempted to eject the cowbird egg while I watched immediately following parasitism (see Appendix); the adults at the other experimentally parasitized nests either did not visit the nest during the first hour or incubated most of the time.

Cost of puncture-ejection.—For the analysis of the cost of puncture-ejection, I assumed that vireo eggs sometimes were damaged as a result of the vireo's bill ricochetting off the thick-shelled cowbird egg and puncturing a vireo egg(s), and not because the vireos mistook their own eggs for cowbird eggs. Including the case of rejection by desertion, Warbling Vireos lost or damaged 5 of their own eggs (from nests 93-4 and 93-8), while rejecting 17 cowbird eggs (Table 1), or 0.29 vireo eggs for every cowbird egg rejected. Excluding the deserted nest, I estimated this figure to be 0.13 vireo eggs per cowbird egg ejected. Considering all 16 Northern Oriole ejections of cowbird eggs and the 6 oriole eggs lost or damaged, I estimated that 0.38 oriole eggs were lost or damaged for every cowbird egg ejected (see Sealy and Neudorf 1995). Comparison of nests with host-egg damage, including the deserted nest (2 of 17 Warbling Vireo nests; 6 of 16 Northern Oriole nests), showed that Warbling Vireos were not more likely to damage their own eggs in nests when they rejected cowbird eggs than did Northern Orioles (Fisher exact test, $P = 0.118$). Excluding the deserted nest, comparison of this incidence (1 of 16 Warbling Vireo nests; 6 of 16 Northern Oriole nests) showed also that Warbling Vireos did not damage more of their own eggs when they ejected cowbird eggs than did Northern Orioles (Fisher exact test, $P = 0.083$).

DISCUSSION

Evolution of rejection behavior.—Evolutionary lag is reasonable according to basic theory, but it is probably impossible to confirm as the cause of a trait's absence. Host responses to brood parasitism, however, provide some of the best opportunities to do so (Rothstein 1990). Despite their small size, Warbling Vireos ejected cowbird eggs (Table 1) and incurred little cost for this ejection relative to the potentially huge costs of parasitism. Indeed, Warbling Vireos typically lose their entire brood if they accept a cowbird egg (e.g. King 1954, Marshall 1957, Schultz 1958, Rothstein et al. 1980, Cannings et al. 1987, C. P. Ortega pers. comm., D. Ward pers. comm.). Rothstein (1975a, 1982) argued that rejection would be feasible for accepter species and that the absence of egg ejection, or an alternative method of rejection, such as nest desertion or egg burial, represents evolutionary lag. Small species that accept a cowbird egg, therefore, do so because of evolutionary lag, and not because acceptance is less costly and, hence, more adaptive than rejection.

Rohwer and Spaw (1988) argued against this view, pointing out that accepter species tend to be smaller than egg ejecters and, therefore, should encounter difficulty and incur greater costs during ejection of thick-shelled cowbird eggs. Rohwer and Spaw (1988) noted that small accepter species may be able to lift cowbird eggs only by puncturing them, behavior that puts their own eggs at risk. Puncture-ejection of cowbird eggs by Warbling Vireos, at so little cost, suggests that thick-shelled eggs alone do not prevent small hosts from puncturing and removing cowbird eggs. However, the relationship between host size and ejection cost may not be a linear one. A threshold may exist where species with the high costs of ejection average smaller than those with the low costs. The Warbling Vireo may be at or near the minimum value for size of an ejecter species. If the relationship is linear, then the results of my study, by default, support the evolutionary-lag hypothesis because the cost of ejection was no more for the smaller species (Warbling Vireo) than for the larger species (Northern Oriole). A shortcoming of my study, however, is that only two host species were tested. Hence, rejection of the equilibrium hypothesis is weak.

Other small passerines in addition to Warbling Vireos are known to be able to puncture

TABLE 2. Parasitism frequencies on Warbling Vireos by Brown-headed Cowbirds.

Locality	No. nests examined	Percent nests parasitized	Source
Populations west of Great Plains			
British Columbia	43	79.1[a]	Cannings et al. (1987)
British Columbia	4	75.0	Campbell and Meugens (1971)
Wyoming	2	50.0	Hanka (1979)
California	5	80.0	Rothstein et al. (1980)
Populations in and east of Great Plains			
Manitoba	56	3.6	This study
Kansas	17	0.0	Johnston (1964)
Illinois[b]	19	0.0	Graber et al. (1985)
Ontario	55	10.9	Peck and James (1987)
Québec[c]	8	0.0	Terrill (1961)
Michigan	7	0.0	Sutton (1949)

[a] In on-going study of reproductive success of Warbling Vireos in southern Okanagan Valley, British Columbia, David Ward (pers. comm.) recorded parasitism on 50 to 80% of about 60 nests examined, and cowbird eggs were accepted in nests that did not fail before acceptance could be determined.

[b] Poling (1889:134) stated that in "large number" of Warbling Vireo sets from Quincy [Illinois] area, three had cowbird eggs.

[c] Single nest, examined in Montreal area, was not parasitized, nor were "several others examined" by Napier Smith at Magog (Stranstead County, Québec). No clutches from Napier collection and two additional clutches in Canadian Museum of Nature were parasitized. However, Terrill (1961:6) reported Warbling Vireo feeding "well-fledged" cowbird on 9 August 1956.

cowbird eggs. Marsh Wrens (*Cistothorus palustris*)—puncture specialists that sometimes eject broken eggs, including those of their own species (Picman 1977)—can puncture cowbird eggs, but they have greater difficulty puncturing them than the thinner-shelled eggs of various other passerines (Spaw and Rohwer 1987). Many small passerines puncture-eject eggs of the Common Cuckoo (*Cuculus canorus*; Davies and Brooke 1988, Lotem et al. 1992), but this comparison may not be valid because, unlike cowbird egg shells, those of *Cuculus* are not proportionately thicker than the shells of their hosts (Brooker and Brooker 1991). Because Marsh Wrens and small cuckoo hosts puncture-eject parasitic eggs, but no small cowbird host was known to eject them, Rohwer et al. (1989) conjectured that, if puncture-ejection is not unduly difficult to evolve, this form of ejection must be prohibitively costly to cowbird hosts.

General body size may not be the only characteristic that determines the capacity for a bird to eject eggs from its nest. Bill type and size (Rothstein 1975a), ability to grasp the broken edge of the punctured egg (Kemal and Rothstein 1988), leverage and neck strength, and depth of nest (Rothstein 1977, Rohwer et al. 1989) may have roles in this behavior.

Geographic variation in host responses.—Observations suggest that individuals in some populations of Warbling Vireos do not reject cowbird eggs (Table 2). Friedmann et al. (1977) indicated that in the absence of experimental data, a species can be assumed to be an accepter if 20% or more of its nests are naturally parasitized and if this parasitism is always, or nearly always, accepted. This cut-off seems justified because in most ejecter species, 80 to 100% of all individuals eject cowbird eggs (Rothstein 1975a). Also, few records of natural parasitism of known ejecters exist, or parasitism is generally reported at frequencies less than 10% (e.g. Friedmann et al. 1977, Rothstein 1975b, Scott 1977, Rich and Rothstein 1985, Sealy and Bazin 1995). In populations of the Warbling Vireo west of the Great Plains, frequencies of cowbird parasitism greater than 50% have been recorded, whereas frequencies of parasitism on populations in and east of the Great Plains, including Delta Marsh, all are under 11% (Table 2). According to the criterion of Friedmann et al. (1977), Warbling Vireos in western populations accept cowbird eggs, whereas those in central and eastern populations apparently reject them. The low frequency of parasitism on Warbling Vireos in populations in central and eastern North America compared with those recorded in western North America, however, may reflect differences in frequency of parasitism, differences in host rejection, or both. Parasitism on ejecter hosts may go undetected if rejection occurs before nests are inspected by the researcher (Scott 1977, Sealy and Bazin 1995). Experimental parasitism on the Warbling Vireo throughout its breeding

range is needed before the status of individuals in different populations as rejecters or accepters becomes known.

The apparent geographic variation in responses to cowbird parasitism makes the Warbling Vireo unique among cowbird hosts whose accepter/rejecter status has been determined experimentally. This species, however, apparently consists of two sibling species, one species that breeds west of the Great Plains area and the other that breeds in central and eastern North America. The Warbling Vireo is listed as a single species by the American Ornithologists' Union (1983) with four subspecies recognized (AOU 1957), although their distributional limits are known only roughly (e.g. Sibley 1940, Phillips et al. 1964, Worthern 1969). One western subspecies, *V. g. swainsonii*, meets the nominate subspecies, *V. g. gilvus*, in west-central Alberta, but the two forms apparently do not interbreed (W. B. McGillivray and J. C. Barlow pers. comm.). Sibley and Monroe (1990) considered the two subspecies to be separate species, the Western Warbling Vireo (*V. swainsonii*) and Eastern Warbling Vireo (*V. gilvus*). Thus, individuals of *V. swainsonii* apparently accept cowbird eggs, but those of *V. gilvus* do not. Interestingly, *swainsonii* averages slightly smaller than *gilvus* in body measurements, including the bill (Ridgway 1904), and in mass (12 g; Dunning 1984). In addition to having been in contact with cowbirds for a much shorter period of time (see Mayfield 1965, Rothstein 1994), *V. g. swainsonii* also may be just below the minimum size value for species that eject cowbird eggs. Nest desertion, however, should be an option for parasitized individuals of *swainsonii*, but this behavior has not been reported. Frequency of parasitism on *swainsonii* has been reported from 50 to 80% (Table 2). It would be interesting to parasitize nests of *swainsonii* and *gilvus* where these forms co-occur (i.e. west-central Alberta). According to the evolutionary-lag hypothesis, individuals of both species should exhibit rejection there, assuming each species has been in contact with cowbirds for similarly long periods of time.

Because parasitized Warbling Vireos usually rear only cowbirds, rejection is better than acceptance and the vireos would be expected to become rejecters. My results confirm this prediction. Rothstein (1975b) stated that, when an accepter species is parasitized at a high frequency (40 to 80% of nests parasitized), selection would be expected to change it to a rejecter

within 100 years or less (see also Arias-de-Reyna and Hildalgo 1982, Nakamura 1990, pers. comm.). Unfortunately, it is not known at what frequency cowbirds historically parasitized Warbling Vireos at the Delta Marsh or how long the rejecter genes took to spread through the population. If individuals in populations of Warbling Vireos in eastern North America, however, also reject cowbird eggs, presumably rejecter genes became fixed in those populations in less than the 200 years since cowbirds colonized eastern North America (see Mayfield 1965).

Davies and Brooke (1989) noted that rejection behavior is not constrained by systematic position, but rather evolves when a species is likely to have been exploited by a brood parasite. Although many vireo species are parasitized at frequencies greater than 80% (e.g. Barlow 1962, Southern 1958, Goertz 1977, Grzybowski et al. 1986, Marvil and Cruz 1989), none is known to eject cowbird eggs, even though some of these species rear only cowbirds when parasitized. Perhaps species that do not puncture-eject cowbird eggs have tried, in the evolutionary sense, but the behavior may have been selected against.

Although Rothstein (1970:104–105) recorded ejection of one of three artifical cowbird eggs placed in Red-eyed Vireo (*V. olivaceus*) nests, this species has never been reported ejecting cowbird eggs despite hundreds of observed cases of natural parasitism on it (e.g. Sutton 1949, Southern 1958, Terrill 1961, Southern and Southern 1980). Red-eyed Vireos often desert parasitized nests (Graham 1988), but experiments are required to establish whether the response actually is to the parasitism (see Hill and Sealy 1994). Friedmann (1963:37) included the Bell's Vireo (*V. bellii*) in a list of host species known or suspected to eject cowbird eggs, possibly on the basis of three cases of ejection suspected by Mumford (1952) and Barlow (1962). Other workers studying Bell's Vireos have not mentioned ejection of cowbird eggs, although desertion of parasitized nests occurred occasionally (e.g. Pitelka and Koestner 1942, Nolan 1960). Wiley (1982:136) recorded ejection of an artificial Shiny Cowbird (*M. bonariensis*) egg at one of three Black-whiskered Vireo (*V. altioguus*) nests artificially parasitized in Puerto Rico. Interestingly, Shiny Cowbirds have colonized Puerto Rico within the last 35 years (Cruz et al. 1985).

In conclusion, I have shown that individuals in one population of Warbling Vireos reject

cowbird eggs by puncture-ejection. No other species of vireo is known to eject cowbird eggs, although responses of other species to experimentally introduced cowbird eggs are required. My results, therefore, are consistent with the evolutionary-lag hypothesis. The family Vireonidae provides an excellent opportunity to test the equilibrium hypothesis because: (1) phylogeny is controlled; (2) there is a range, albeit small, of body sizes; and (3) populations of some species are parasitized at very high levels.

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APPENDIX

OBSERVATIONS OF REJECTION BEHAVIOR BY WARBLING VIREOS

Case of desertion.—Warbling Vireos deserted one experimentally parasitized nest (93-4) after two vireo eggs had been removed, possibly removed by the vireos (Table 1). I parasitized this nest at 0729 on the day it received its fourth egg. Although no vireo flushed from the nest when I parasitized it, from less than 5 m away the female uttered alarm calls and the male sang intermittently. During the observation bout

that followed parasitism, both vireos spent most of their time 5 to 10 m from the nest, the male singing while both individuals called occasionally. Once, the male approached to within about 10 cm of the nest, but did not look into the nest. At 0806 he returned and peered into the nest but left after 1 to 2 s. Neither vireo visited the nest again during the observation bout. Only the undamaged cowbird egg and two vireo eggs were in the nest 4 h later. I did not detect any adults near the nest then, nor on either of the inspections on each of the next two mornings.

I believe that the vireos deserted this nest because of the "parasitism." One of the vireos may have broken both of the eggs while it tried to puncture the cowbird egg, removed the broken eggs (Kemal and Rothstein 1988), and then abandoned the nest in response to the reduced clutch size (see Rothstein 1982). Warbling Vireos are known to remove their own eggs when damaged by cowbirds (Riegel 1954). Also, a vireo may have removed its own eggs by mistake and then abandoned the nest.

Ejection by spiking.—During the observation bouts, four females ejected the cowbird eggs from their nests (92-3, 93-5, 93-9, 93-17). Observations at nests 92-3 and 93-5 illustrate ejection preceded by spiking and breakage, respectively. At 0810, after flushing the female (marked by a twisted tertial) from nest 92-3, I parasitized the nest while the female uttered alarm calls. About 4 min after the parasitism, the female moved slowly along the nest branch to the edge of the nest, several times looked into it, and then looked away, each motion lasting for 1 to 2 s. At 0815, the female pecked vigorously for 7 to 8 s at an object in the nest, presumably the cowbird egg, then circled the nest and re-entered it at the same position as above. She repeated this behavior many times, until at 0823 she left the nest for 65 s and uttered alarm calls intermittently. Upon returning, the female repeated the above behavior, pecking the egg and then circling the nest, over and over again. Finally, after repeating this behavior 17 times, the female ingested something, and at 0828 punctured the egg shell with her bill, lifted the egg out of the nest, and carried it away, arcing toward the ground as she flew. She dropped the egg about 2 m above a road. About 5 s later the female returned to the nest and incubated the four eggs (later determined to be unsoiled and undamaged) continuously for the next 15 min. I neither saw nor heard the male during the entire episode.

At nest 93-5, the vireo broke the cowbird egg into at least two pieces, consumed some of the contents, and then carried away each piece separately (one piece 5 m away, the other 8 m). At 0750, I inserted a cowbird egg into the nest, after flushing the female from the nest. About 1 min after the parasitism, she returned to the nest and immediately began to peck at the eggs. Some pecks against the egg were delivered with such force that I could hear them from 7 m away. The female pecked the egg eight to nine times from one

position on the nest rim, and then moved to the other side of the nest and repeated the procedure several times until she broke the cowbird egg. After mandibulating tiny pieces of eggshell, she ingested some albumen. At 0809, the female flew downward from the nest, which was only 1.7 m high, carrying a tiny piece of eggshell in her beak, which she dropped. Immediately after she left the nest the male entered it and incubated, sang intermittently over the next 30 s, and incubated silently until 0817 when he left as the female returned to the nest. The female pecked the egg, as before. At 0822, she picked up a piece of eggshell and flew with it upward out of sight into the canopy. A few seconds later, she returned to the nest, pecked once, picked up the remainder of the cowbird egg and carried it to a low branch, and dropped it. The female then flew back to the nest and, without hesitating, incubated while the male sang in the canopy above the nest. Over the next 15 min, she incubated continuously except for absences of 42 and 37 s. I later checked the eggs and found that none had been damaged or soiled.

Attempted ejection by males.—At two nests (93-3, 93-11), males attempted to eject the cowbird egg while I watched. Observations at nest 93-11 illustrate this behavior. While the male (with a metal band) sang in the canopy, and the female was out of sight, I parasitized the nest at 0715. At 0718, the male perched on the edge of the nest, peered into it, sang once and then entered the nest to incubate, singing every 5 to 6 s. About 50 s later, the male rose in the nest and pecked vigorously at an egg. Bouts of pecking and singing followed and, at 0722, the male stood on the edge of the nest and continued with bouts of three to four pecks, pauses, and singing until, at 0724, he flew into the canopy of a neighboring tree, but within a few seconds returned to within 5 m of the nest. Here he stayed for 6 min before approaching the nest and peering into it for a few seconds. He then flew to another tree and sang. At 0731, the female stood on the edge of the nest for about 60 s and then began to incubate. Soon she peered beneath herself and pecked an egg. She did this intermittently until she left the nest at 0749. Over the next 5 min, the female twice visited the nest and arranged nesting material but did not peck an egg. For the duration of the observation bout, the female alternatively foraged and incubated but did not peck an egg.