

BROOD PARASITISM, NEST PREDATION, AND SEASON-LONG REPRODUCTIVE SUCCESS OF A TROPICAL ISLAND ENDEMIC¹

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Abstract. The Puerto Rican Vireo (*Vireo latimeri*) is a single-island endemic resident on Puerto Rico. The Shiny Cowbird (*Molothrus bonariensis*), a generalist brood parasite native to South America, arrived on the island in 1955 and has established itself as a breeding resident. To determine the impact of the exotic cowbird on vireo reproductive success, I studied the demography of marked Puerto Rican Vireos in Guánica Forest, Puerto Rico, in 1990–1993. Vireo breeding season length varied among years (69–106 days), apparently influenced by rainfall. The primary causes of reproductive failure were nest parasitism and nest predation. Cowbirds parasitized 73–83% of vireo nests. Parasitism reduced the number of vireos fledged per successful nest by 82%, primarily through decreased hatching success and fledging success. Vireos did not abandon nests in response to cowbird egg-laying, but frequently deserted if cowbirds removed host eggs. Native avian predators and exotic mammalian predators together caused the demise of about 70% of all nest attempts. As a result, daily nest survival rate was low (0.93 ± 0.01), and only 13–19% of nests fledged vireo or cowbird young. Pairs renested after failure and attempted to raise second broods. Females in this population attempted two to six nests per season and fledged an average of 1.33 vireos in 1991 and 0.24 vireos in 1993. The combination of restricted breeding season, high predation and parasitism rates, large impact of parasitism on reproductive output, and low seasonal fecundity of females suggests that, despite high survival rates, the Puerto Rican Vireo is in danger of extirpation from portions of its range.

Key words: *Vireo latimeri*, *Molothrus bonariensis*, Puerto Rican Vireo, Shiny Cowbird, demography, reproductive success, brood parasitism.

INTRODUCTION

Historically, the major cause of avian extinctions on islands has been the accidental or intentional introduction of exotic species (King 1985). Because many island birds have evolved in isolation from predators, disease, and competitors, they often are poorly equipped to deal with these agents when they are introduced (reviewed in Moors 1985).

Puerto Rico is home to twelve single-island and six regional endemic birds (Raffaele 1989). The Shiny Cowbird (*Molothrus bonariensis*), a generalist avian brood parasite native to South America, Trinidad, and Tobago, arrived on the island in about 1955 (Post and Wiley 1977b) and is now common in many parts of the island. The cowbird forages communally in agricultural areas, pastures, and animal feedlots, and its range expansion was facilitated by widespread clearing of forests for agriculture and livestock

throughout the West Indies in the early 1900s (Post and Wiley 1977b).

Since its arrival in Puerto Rico, the Shiny Cowbird has established itself as a breeding resident, parasitizing at least 17 species (Wiley 1985, Pérez-Rivera 1986, Post et al. 1990), including the Puerto Rican Vireo (*Vireo latimeri*, hereafter PRVI) (Pérez-Rivera 1986). The PRVI is a small (11–12 g), nonmigratory tropical island species in the White-eyed Vireo (*V. griseus*) group. As a single-island endemic, the PRVI has a restricted range (Raffaele 1989). Many vireos in North America are particularly susceptible to parasitism by the Brown-headed Cowbird (*M. ater*), suffering high rates of parasitism and poor reproductive success because of cowbirds (e.g., Martin 1992, Grzybowski 1995). Small birds may suffer particularly high reproductive losses from parasitism because their young are out-competed by the larger parasitic young (Friedmann 1963, Rothstein 1990). Furthermore, parasitic birds did not exist previously in the Antilles, and so it is unlikely that native birds would have evolved behavioral defenses against brood parasitism (Wiley 1985). The ability of parasitism to severely affect new-

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ly-exposed host populations is well documented. Thus, the invasion of the Shiny Cowbird is cause for concern for the future of the PRVI.

In addition to the introduced cowbird, Puerto Rico's native avifauna also must contend with a variety of introduced mammals which act as predators on eggs, young, and adults. These include rats (*Rattus* spp.), mongooses (*Herpestes auropunctatus*), and feral cats (*Felis domesticus*) (pers. observ.).

Abundance of the Puerto Rican Vireo in Guánica Forest, Puerto Rico's largest dry forest reserve, has declined steadily over the last decade (Faaborg et al. 1997). To determine the impact of the introduced cowbird and nest predators on the endemic vireo, I studied the demography and season-long reproductive success of the Puerto Rican Vireo over three years and four study areas in Guánica Forest. Previous published information on the breeding ecology of this species was limited to six nests described by Spaulding (1937). This work assesses the effects of parasitism and predation on the reproductive success of the vireo, provides one of the few intensive accounts of the seasonal fecundity of a tropical passerine, and provides demographic information needed to determine the prospects for long-term persistence of this species.

METHODS

STUDY AREA

Guánica Commonwealth Forest Reserve (17°55'N, 67°05'W), on the southwest coast of Puerto Rico, comprises 4,015 ha of mature dry subtropical forest over shallow limestone soils. Rainfall is variable and averages 860 mm annually. There is a pronounced dry season from December to March, a short rainy season from April to May, and heavy rains from August through November (Murphy and Lugo 1986). The Shiny Cowbird was first recorded in Guánica Forest in 1969 (Kepler and Kepler 1970). Detailed information on the breeding bird community can be found in Woodworth (1995).

Research was conducted in four study areas, approximately 50-ha each, in the Forest's 2,000-ha eastern tract. The Couto and Julio Velez study areas are typical of pristine subtropical forest in the region, and dominant trees include *Bucida buceras*, *Pisonia albida*, *Bursera simaruba*, *Exostema caribaeum*, and *Guaiacum officinale*. *Amyris elemifera*, *Ateramnus lucidus*,

Croton spp., and *Eugenia* spp. are common in the understory. These study areas are characterized by high shrub density and a short (7–8 m), relatively open canopy. The Ballena and La Hoya study areas are recovering from human disturbance. The La Hoya study area is second-growth forest which was exploited for charcoal production and fence-posts before 1930. A little over one-half (31 ha) of the Ballena study area was planted as an experimental mahogany (*Swietenia mahogoni*) plantation in the 1930s, and *Swietenia* is still the dominant tree species. As a result, Ballena study area contains a greater proportion of tall (15–20 m) trees and a more open understory than undisturbed forest.

BEHAVIORAL OBSERVATIONS

Field work was conducted over three breeding seasons: 12 April–25 July 1990, 1 April–30 August 1991, and 22 March–8 August 1993. Two shorter visits to the study area were made during another breeding season (13–27 June 1992) and one winter (11–21 January 1993).

Resident vireos were captured by using recorded vireo song to lure territorial males or pairs into mist nets. Because males were more aggressive than females toward territorial intruders, the majority (78%, $n = 65$) of birds captured were males. Birds were weighed, measured, examined for molt, and banded with a U.S. Fish and Wildlife Service numbered aluminum leg band and a unique combination of three colored leg bands. Additional birds were captured in mist nets in winter of 1993 (methods in Woodworth et al., in press). In all, 88 Puerto Rican Vireos were color-banded including 51 males, 14 females, 13 fledglings, and 10 adult birds of unknown sex (winter captures).

Behavioral observations were made by following focal individuals and recording behavior on a hand-held cassette recorder or field notebook. Territorial boundaries were determined by recording all sightings of color-marked birds, nests, song perches, and boundary disputes on 1:2500 scale maps of the study areas. The mated status of territorial males was determined by following focal individuals until mated status could be confirmed or until a minimum of 90 min of "track time" had elapsed (following Probst and Hayes 1987; see Woodworth 1995). Because males and females took turns incubating the eggs, they were rarely seen together after incubation had begun. Thus, males had to be under

observation for at least 45 continuous minutes per observation bout (average incubation bout was approx. 30 min; Woodworth, unpubl. data) to avoid misclassifying a male as unmated who actually had an incubating mate.

BREEDING SEASON

The length of the breeding season was defined as the interval between the dates when 50% of females began breeding (building their first nest of the season) and when 50% of females left breeding condition (no longer initiated a new nest after nest failure or fledging) (Nolan 1978, Pease and Grzybowski 1995). Presence of molt was taken as corroborating, but not definitive, evidence that a bird had ceased to breed, because a small percentage of individuals (3.1–8.5%) of tropical species may overlap breeding and molting activities (e.g., Foster 1975, Ralph and Fancy 1994). A female that fledged a brood and did not renest was considered to have left breeding condition 13 days after her young fledged (the median time elapsed between fledging young and renesting in this study). Females that disappeared from their territories before the end of the breeding season were excluded from analysis.

NEST SUCCESS

Nests were located by observing mated pairs and following individuals to the nest. Each nest was plotted on a field map and checked regularly to document breeding biology, parasitism, and nest outcome. Nest check intervals varied from 1–9 days, depending on the stage of the nest (median nest check interval was 2 days). Chicks were banded on the eighth day after hatching, and further nest checks were made from a distance to avoid causing premature fledging.

Transition dates (egg-laying, incubation, hatching, fledging, failure) were determined from direct observation or by back-dating or forward-dating from other known events in the breeding cycle, assuming (1) an average nest-building period of 9.5 days, (2) one host egg laid per day, (3) a clutch size of 2–3 eggs, (4) incubation periods of 15 days for vireo chicks and 11.5 days for cowbird chicks, and (5) nestling periods of 12 and 13 days for vireos and cowbirds, respectively (Woodworth 1995). I used information from the stage of nest-building, pair behavior, "candled" eggs, embryos from destroyed nests, chick measurements along with

regressions for chicks of known age (Woodworth, unpubl. data), and mobility of chicks out of the nest to make the most accurate judgments possible. If no other data were available, I assumed the transition occurred at the midpoint of the nest check interval (Mayfield 1975). I defined incubation as beginning on the day the last host egg was laid. A nest was considered successful if it fledged either a vireo or a cowbird chick. I verified success by locating parents and fledglings; one unconfirmed case was assumed to have fledged.

Daily nest survival rates, period survival probabilities, and their associated variances were calculated by the Mayfield method (1975). Exposure days for the egg stage began with the laying of the first egg, whether host or parasite, and lasted until any egg, host or parasite, hatched. Because Puerto Rican Vireos begin incubation with the laying of the first egg (Woodworth, unpubl. data), nest success calculations for egg-laying and incubation were combined.

Success of nests found and revisited might differ from that of nests that are not subject to human disturbance (reviewed in Götmark 1992), and I handled this in several ways. First, field protocol was designed to minimize disturbance to the birds and cues for predators (*sensu* Hannon et al. 1993, Martin and Geupel 1993). Second, I excluded from analysis any nests where human disturbance was excessive (e.g., photography, experiments), regardless of the outcome of the nest. Third, I compared the total nest life (initiation of building to failure) between the nests I located and nests I knew of but was unable to locate. Finally, I examined the data for evidence of human-caused increase in failure rates, following Hannon et al. (1993). I matched each depredated nest to a sample of successful nests matched for the date the nest was found and nest height (which influenced success rate, Woodworth, unpubl. data). I then used a Wilcoxon's signed-ranks test (Sokal and Rohlf 1981) on the percentile score for the number of visits made to depredated vs. successful nests, and checked for an effect of visitation, considering (1) all visits to the nest, whether or not the nest was approached, (2) visits where the attending bird was flushed, and (3) visits during which the contents of the nest were handled.

BROOD PARASITISM

Brood parasitism rates were calculated as the *seasonal parasitism fraction*, the proportion of

all nest attempts in an entire breeding season that were parasitized, and the *daily (instantaneous) parasitism rate*, the rate at which cowbird eggs were laid in susceptible nests per day (Pease and Grzybowski 1995). The "window of susceptibility to parasitism" is that period of the nesting cycle when an individual nest is susceptible to parasitism (Pease and Grzybowski 1995). I documented the dates of laying of cowbird eggs in relation to host clutch initiation and defined the window as that period when $\geq 90\%$ of cowbird eggs were deposited in the nest.

For calculating the seasonal parasitism fraction, I included only nests which met the following criteria:

(1) The nest was found before or on the first day of egg-laying. Using nests found at a later stage would introduce bias for two reasons: first, parasitized and unparasitized nests may differ in average active nest life, as found for the Prairie Warbler (Nolan 1978), and thus a sample of nests found later in the nesting cycle may be biased towards unparasitized nests. Second, egg ejection or partial predation might cause a parasitism event to go undetected in a sample of nests found in later stages (Rothstein 1975a).

(2) The nest was active throughout the window of susceptibility to parasitism. Abandonment or predation during the "window" may forestall parasitism that would otherwise have occurred or might cause a cowbird egg to go undetected. For host species which desert in response to cowbird interference, this rule will bias the estimated parasitism rate downwards, because nests in which cowbirds caused desertion before clutch completion would not be counted (Nolan 1978), but Puerto Rican Vireos did not abandon nests in response to parasitism in this study.

(3) Cowbirds had no role in helping the field worker locate the nest. Inclusion of nests found with the help of cowbirds would usually be parasitized, and would bias the estimate upward.

(4) The parasitism status had been recorded before the nest was disturbed by a predator. In some cases, cowbird eggs or fragments were found beneath a depredated nest, and this nest could probably have been safely assumed to have been parasitized. However, other nests were found depredated with only vireo egg fragments or no fragments remaining, and their parasitism status could not be accurately ascertained. To include the former in calculations and

exclude the later would be to bias parasitism rates upwards. Conversely, to include the former as parasitized and the later as unparasitized would bias rates downward. To avoid this dilemma, all such nests were excluded.

The daily parasitism rate was calculated by tallying the total number of cowbird eggs laid during the window of susceptibility to parasitism, and dividing by the total number of days on which nests were examined (nest-days) during the window (Nolan 1978). The standard error was calculated assuming binomial sampling. Nests which were completed but which never received a host egg were assumed to have been exposed to parasitism for 2 days of the window of susceptibility (as in Pease and Grzybowski 1995). Egg-laying by the Puerto Rican Vireo is generally preceded by a one- to four-day period of "inactive building," when the nest is complete (Woodworth, unpubl. data); 18–20% of cowbird eggs were laid during this period in the present study.

The daily parasitism rate calculation allowed incorporation of data on nests only observed for a portion of the susceptible period, and is analogous to the Mayfield method for calculating daily nest survival rates (Mayfield 1975). Mayfield's method is subject to bias if the interval between nest checks is long (Johnson 1979), but this bias should be minimal in the present case, where the median nest check interval was 2 days. A second bias arises if a field worker cannot distinguish two events from one occurring in a single interval (e.g., a second cowbird removed the egg of the first). In this study, nest check intervals were relatively short, and egg-removal relatively rare, and so I believe the bias caused by this was small. Finally, bias would occur if nest predation and parasitism occurred in the same interval, and the parasitism was therefore missed. I avoided this bias by tallying "observation days" only until the last day that the nest was observed to be active, or the end of the window, whichever was first. This is a crucial difference from the Mayfield method for calculating daily nest survival rates, which would include in the tally one-half of the time since the last observation (Mayfield 1975). The daily parasitism rate can be used, along with other measures of daily nest survival rates and productivity, to calculate the expected seasonal fecundity of females (Pease and Grzybowski 1995).

BEHAVIORAL RESPONSE TO PARASITISM

I investigated vireos' responses to two types of cowbird disturbance at the nest, cowbird egg-laying and host egg-removal, by examining the data for cases of acceptance (the cowbird egg remained and nesting activities continued normally), ejection (the cowbird egg disappeared or was punctured), or abandonment (the nest was unattended for two or more consecutive visits). Because of high rates of nest predation in this study, I used a criterion of 2 days for determining host response. Using a criteria of 5 days (Rothstein 1975a) did not change the overall results. Although Puerto Rican Vireos begin incubation with the laying of the first egg (Woodworth, unpubl. data), I wanted to distinguish between responses on days when host eggs were actively being added to a clutch and those when they were not. Therefore, for this analysis only, egg-laying was defined as including the 2–3 days when host eggs were laid, and incubation was defined as beginning the day after the last host egg was laid.

SEASON-LONG REPRODUCTIVE SUCCESS

To obtain values for season-long reproductive success of females, I followed individual pairs through successive nesting attempts. I included pairs with at least one marked member and which were followed throughout the entire breeding season. A pair's typical behavior after nest failure was to begin nest-building again the following morning. The time elapsed was considered insufficient for new pair formation, and in cases with only one marked member this was used as circumstantial evidence that a mate switch had not occurred. In three pairs the unmarked member of a pair wore a single aluminum band which served as an added check for mate switches. Finally, the behavior of each pair with an unmarked member was scrutinized for male advertising behavior or ritualized pairing behavior. I excluded one pair in which a mate-switch possibly occurred, four females which disappeared from their territory at the end of the season and which may have bred elsewhere, five pairs for which the outcome of the last nest attempt of the season was not known, two pairs which experienced excessive human disturbance at one of their nests, regardless of the outcome of that nest, and seven pairs because I failed to locate one or more of their nests. Thus, final

calculations were made using 23 pairs (6 pairs in 1991 and 17 in 1993).

The possibility exists that reproductive success of the females I was able to follow for an entire breeding season differed from that of females I could not follow. The probability of following a female for an entire season could be expected to decrease the more nests she built, because with each new nest the observer ran the risk of not finding the nest. I was more likely to have entire breeding season data for a female with at least one successful nest, because it was easier to monitor a known nest than find a new one. Such a bias would tend to inflate my estimate of reproductive success.

STATISTICAL ANALYSIS

For statistical analyses, an alpha level of 0.05 was required to conclude significance; all tests are two-tailed unless otherwise stated. For comparisons among three or more survival rates, daily nest survival rates, or parasitism rates, I used the program CONTRAST (Hines and Sauer 1989), which uses the chi-square statistic proposed by Sauer and Williams (1989). Criteria for inclusion of a nest in a sample varied depending upon the analysis, and therefore sample sizes varied among analyses. In order to avoid certain biases, many, but not all tests, required that the nest had been found before or on the first day of egg-laying (Mayfield 1975). Most samples had further requirements specific to the analyses; sample size and criteria for inclusion are presented with each analysis or as a footnote to the relevant table. Values presented are means \pm SD.

RESULTS

Observations were made on 10, 25, and 42 territories in 1990, 1991 and 1993, respectively. Over the three years of the study, an average of 87% (70–92%) of males on the study areas were mated ($n = 71$, and includes 6 males which wore only an aluminum leg band). A total of 156 nests was found. These nests represent the nest attempts of 45 pairs (10 followed for two or more seasons) and 5 partial nests built by 4 unmated males. Almost all nests (137; 88%) were found before or on the first day of egg-laying. Of these 137 nests, 98 received at least one host egg, 77 could be assigned parasitism status without ambiguity, and final nest outcome was known for 133 nests.

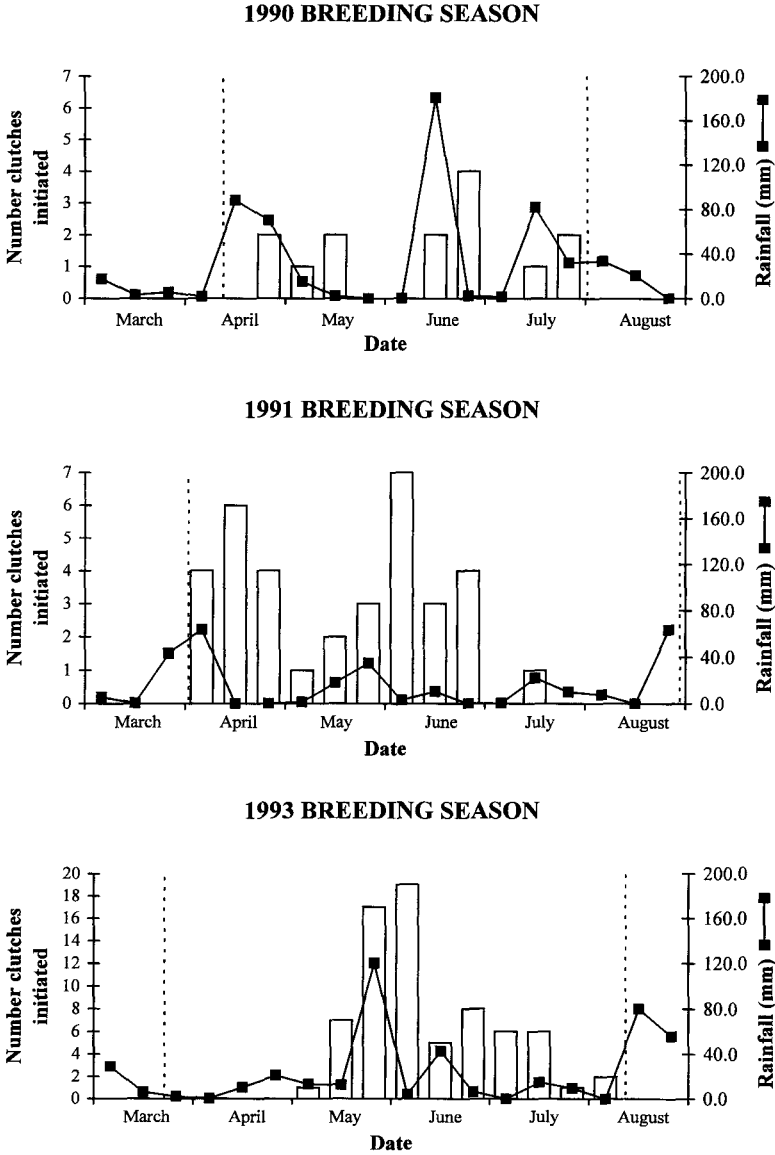


FIGURE 1. Dates of Puerto Rican Vireo clutch initiation in relation to rainfall, Guánica Forest, Puerto Rico, March–August 1990, 1991 and 1993. Each month was divided into three 10–11-day periods. Bars represent clutch initiations and solid lines represent rainfall. Vertical dotted lines bracket the beginning and end of each field season.

BREEDING SEASON

Eggs were laid from the second week in April (earliest date: 8 April 1991) to the last week in July or first week in August (latest date: 1 August 1993) (Fig. 1). I infer that the start of the 1991 breeding season coincided with my arrival on the study area at the beginning of April, because: (a) all 9 pairs under observation initiated

nest-building from the 1st to the 14th of April, and (b) 5 additional groups of fledglings, when backdated, indicated initiations during the first two weeks of April. Further indirect evidence includes the fact that rainfall in March 1991 was well below average (Woodworth 1995) and that, to my knowledge, no March breeding records exist for Puerto Rican Vireos on the arid south

coast of Puerto Rico. In 1991, the first birds began nest-building on 1 April, 50% of females were building nests by 4 April, and all females were breeding by 17 April ($n = 9$ females under observation).

In 1993, the dry season was prolonged, and no birds bred in April (27 pairs observed for an average of 2.7 hr each). The first nest was begun on 1 May, the day after the first substantial rainfall of the spring (15.5 mm on 30 April 1993; Fig. 1). Fifty percent of females had come into breeding condition by 7 May, and all birds were breeding by 18 May ($n = 27$ females under observation).

The end of the breeding season (when 50% of females that either lost nests or fledged young did not re-nest) was approximately 19 July in 1991 ($n = 10$ pairs under observation) and 15 July in 1993 ($n = 20$). No females were nesting when the field season ended in 1991, and only one pair was still nesting at the end of the 1993 season. With the exception of this pair, females were observed for an average of 2.5 hr (an average of 4.8 hr spent on territory by observers) after their supposed last nest to confirm that they did not re-nest. Thus, in 1991, the breeding season lasted 106 days, and in 1993, 69 days.

BROOD PARASITISM

Timing and extent of parasitism. A high proportion of vireo nests was parasitized on all four study areas (Table 1). Parasitism status could be determined without ambiguity for 77 of the 98 active nests (criteria listed in Methods); 83% of these were parasitized (95% confidence limits: 74.6–91.6%). The daily parasitism rate, 0.194 cowbird eggs laid per susceptible nest per day, corresponds to a seasonal parasitism rate of 73% (assuming binomial sampling; 95% confidence limits: 64.4–79.2%).

Daily parasitism rates did not differ among study areas in either 1991 or 1993 (1991: $\chi^2_1 = 0.08$, $P = 0.78$; 1993: $\chi^2_3 = 0.38$, $P = 0.94$). Combining study areas, parasitism rate in 1991 was significantly less than in other years ($\chi^2_1 = 6.5$, $P = 0.01$), but this effect disappeared if April nests were removed ($\chi^2_1 = 3.8$, $P = 0.53$). Data from 1991, when breeding began in April, suggest that nests initiated early in the season may be less likely to be parasitized than those initiated later. Before 1 May, 20% of nests were parasitized ($n = 5$); after 1 May, 82% of nests were parasitized ($\chi^2_1 = 6.5$, $n = 17$, $P = 0.008$).

TABLE 1. Frequency of parasitism in Puerto Rican Vireo (*Vireo latimeri*) nests, Guánica Forest, Puerto Rico, 1990–1993.

Measure of parasite activity	Year and study area						Total
	1990		1991		1993		
	Ballena	Couto	Ballena	Couto	J. Velez	La Hoya	
Unparasitized nests ^a	0	0	2	2	1	1	13
Parasitized nests ^a	7	4	11	8	15	4	64
Seasonal parasitism fraction ^a	1.00	1.00	0.85	0.80	0.94	0.80	0.83
Exposure days during window of susceptibility to parasitism	36	33	102	53	96	38	480.5
No. parasitism events during window of susceptibility to parasitism	11	4	20	11	21.5	9	93
Daily parasitism rate ^a (days ⁻¹) ± SE	0.306 ± 0.077	0.139 ± 0.031	0.196 ± 0.039	0.206 ± 0.055	0.244 ± 0.043	0.237 ± 0.069	0.194 ± 0.018

^a See Methods for definitions and criteria. Sample includes some nests for which parasitism status was known but final outcome was not; thus sample differs from some other analyses herein.

TABLE 2. Number of Puerto Rican Vireo and Shiny Cowbird chicks fledged from parasitized and unparasitized nests, Guánica Forest, Puerto Rico, 1990–1993.

Parameter measured	Unparasitized nests			Parasitized nests		
	Mean \pm SD	Range	<i>n</i>	Mean \pm SD	Range	<i>n</i>
Active nests						
Vireo chicks fledged	0.50 \pm 1.02	0–3	14	0.08 \pm 0.37	0–2	72
Cowbird chicks fledged				0.14 \pm 0.35	0–1	72
Successful nests						
Vireo chicks fledged	2.33 \pm 0.58	2–3	3	0.43 \pm 0.76	0–2	14
Cowbird chicks fledged				0.71 \pm 0.47	0–1	14

Data for April breeding only are available from Ballena Study Area in 1991. A late start to the 1993 breeding season precluded testing this result with a second year of data.

Cowbirds laid their eggs randomly in Puerto Rican Vireo nests, without regard to previous parasitism status of the nest (test for Poisson distribution, $\lambda = 1.14$ (88/77), $\chi^2_3 = 5.4$, $P = 0.15$). Sixty-four parasitized nests received on average 1.4 ± 0.62 cowbird eggs each; 45 (70%) received 1 cowbird egg, 15 (23%) received 2, and 4 (7%) received 3.

Cowbirds effectively synchronized their egg-laying with that of Puerto Rican Vireos. The date of cowbird egg-laying in relation to initiation of host egg-laying was known to within a one or two-day period for 40 cowbird eggs. From 40 to 55% of cowbird eggs were laid on the first and second days of the host's egg-laying period, and most cowbird eggs (92–100%) were laid within a 6-day period (the "window of susceptibility to parasitism") that began two days before host egg-laying and ended on the first or second day of incubation, depending on clutch size. Because cowbird eggs required only 11.5 days to hatch, compared to 15 days for vireo eggs (Woodworth, unpubl. data), cowbird eggs laid as late as the third day of incubation were assured of sufficient incubation.

Impact of parasitism on vireo reproductive success. On average, successful parasitized nests fledged 82% fewer vireo young than successful unparasitized nests (Table 2). This was due to the combined effects of cowbird egg puncture and removal, decreased hatching success, and decreased fledging success in parasitized nests.

Cowbird egg puncture and removal. Both Brown-headed Cowbirds and Shiny Cowbirds are known to puncture or remove eggs from nests they parasitize (Hoy and Ottow 1964, Scott

et al. 1992). Single eggs disappeared or were punctured during egg-laying or early incubation in 10 of 64 parasitized Puerto Rican Vireo nests (15.6%), for a total of 8 of 173 vireo eggs and 2 of 106 cowbird eggs. In addition, there was no difference in the vireo clutch size of parasitized nests and unparasitized nests in this study (parasitized, excluding eggs known to have been removed by cowbirds: 2.54 ± 0.48 , $n = 64$; unparasitized: 2.62 ± 0.49 , $n = 13$). Thus, egg removal was rare in this population relative to other studies in Puerto Rico (e.g., egg puncturing occurred in 67% of Yellow-shouldered Blackbird, *Agelaius xanthomus*, nests on mainland Puerto Rico; Post and Wiley 1977a).

Decreased hatching success. Hatching success was defined as the proportion of eggs that were in the nest through expected hatch date that hatched. Thus, the sample includes only nests found before egg-laying, which were active through expected hatch date, and for which exact number of vireo eggs laid and exact number hatching was known. Hatching success of vireo eggs in parasitized nests was significantly less than in unparasitized nests. On average, only 38% of vireo eggs in a parasitized nest hatched, whereas 86% of vireo eggs in an unparasitized nest hatched ($n = 14$ parasitized and 6 unparasitized nests; two-sample *t*-test on proportion of eggs hatching (arcsine transformed), equal variances, $t_{18} = 3.5$, $P = 0.003$). Treating each egg as an independent sample, following Martin (1992), gives similar results (parasitized: 14 of 36 eggs hatched; unparasitized: 12 of 14 eggs, $\chi^2_2 = 8.9$, $P = 0.003$). Cowbird eggs are substantially larger than vireo eggs: Puerto Rican Vireo eggs measured 18.24 ± 1.15 mm in length and 13.94 ± 0.31 mm in width ($n = 28$), whereas cowbird eggs measured 20.19 ± 0.90 mm in length and 15.81 ± 0.58 mm in width ($n = 13$).

The presence of cowbird eggs in the nest may interfere with incubation of the vireo eggs, particularly in multiply-parasitized nests.

Decreased fledging success. In six nests that contained both cowbird and vireo young and which escaped predation, none of 11 vireo hatchlings survived. Cowbirds hatched on average 3.5 days earlier than vireos, and by the time vireos hatched (weighing about 1.2 g), cowbird young outweighed them by up to 12 g (Woodworth, unpubl. data). The vireo nestlings often were buried beneath the larger cowbird nestling(s), and always disappeared within 48 hr of hatching. Because the cowbird chick(s) remained in the nest and appeared healthy, I presumed that the vireo young starved or were crushed, and were removed by the adult hosts. Vireo young only fledged from parasitized nests in the rare instances when the cowbird egg did not hatch ($n = 3/59$; sample less than 64 because the outcomes of 5 parasitized nests were unknown) or the cowbird nestling was removed by a predator before the vireo eggs hatched ($n = 1/59$ nests). In contrast, in 10 nests with vireo chicks but without cowbird chicks and escaping predation, none of the 19 vireo chicks died.

Behavioral response to parasitism. Ejection. Single cowbird eggs disappeared from two parasitized Puerto Rican Vireo nests (2/106 cowbird eggs) during the study. It was impossible to discern whether these were removed by a vireo or a cowbird. Also, one unbroken cowbird egg was found directly beneath a vireo nest that was in the laying stage. The vireo may have prevented a cowbird from laying in the nest, the egg may have come from a different nest, or a vireo or cowbird may have removed the egg by grasp ejection. Because PRVIs have small bills, it is unlikely that they would be able to grasp eject a cowbird egg (Rohwer and Spaw 1988).

Nest abandonment. Puerto Rican Vireos abandoned approximately 12.5% of nests that experienced cowbird disturbance (Table 3). In contrast, PRVIs abandoned 33% of completed nests where there was no known cowbird disturbance. The difference was in the opposite direction expected, because nests that were abandoned were less likely to experience disturbance because of their shorter active life. Furthermore, some undetermined proportion of these may have been abandoned due to cowbird interference before egg-laying began (therefore pre-empting cowbird laying and leaving no evidence), or were

TABLE 3. Proportion of Puerto Rican Vireo nests deserted, by stage of nesting cycle and type of Shiny Cowbird interference observed, Guánica Forest, Puerto Rico, 1990–1993. Sample of disturbed nests included nests found before egg-laying, at which cowbird egg-laying or egg-removal was recorded, and which escaped predation for at least two days thereafter.

Nesting stage	Number of deserting/total number related to type of cowbird disturbance				Total
	No disturbance	Cowbird egg laid only	Vireo egg removed only	Cowbird egg laid and vireo egg removed	
Pre-laying (PL)	—	2/7	—	0/2	2/9
PL or EL ^a	—	1/7	—	1/1	2/8
Egg-laying (EL)	—	0/20	1/1	2/8	3/29
EL or Inc ^a	—	0/12	2/4	0/1	2/17
Incubation (Inc)	—	0/9	—	—	0/9
Total disturbed	—	3/55	3/5	3/12	9/72
Total undisturbed	7/21	—	—	—	—

^a Refers to nests where exact stage of nest at time of disturbance (pre-laying [PL] or egg-laying [EL] or incubation [Inc]) could not be determined.

egg-removals that went undetected by the field worker.

There is no evidence to suggest that PRVIs abandoned nests in response to parasite eggs laid in the nest (Table 3). However, nests where egg-removal occurred, accompanied by cowbird egg-laying or not ($n = 18$), were more likely to be abandoned than nests where cowbird eggs were laid but no egg-removal occurred ($n = 60$) ($\chi^2_1 = 5.2$, $P = 0.02$). Disturbances during pre-laying would be expected to elicit abandonment most readily, because the pair has fewer resources committed to the nesting attempt at this stage (as shown for other hosts of the Brown-headed and Shiny Cowbirds; Clark and Robertson 1981, Wiley 1985). However, early cowbird egg-laying did not cause abandonment (Table 3): 18–20% of cowbird eggs were laid before host egg-laying had begun, and the typical behavior for PRVI females was to initiate nest-sitting on the day the cowbird egg appeared ($n = 6/8$ females, 7/9 nests). In all but one case (possibly abandoned prior to cowbird laying), the females eventually laid in the nest and incubated normally.

NEST SUCCESS

Daily and overall nest survival rates for Puerto Rican Vireo nests were low (Table 4). Daily nest survival rates did not differ between the egg and nestling stages of the nesting cycle ($\chi^2_1 = 1.1$,

TABLE 4. Daily and overall nest survival rates of Puerto Rican Vireo nests in Guánica Forest, Puerto Rico, 1990–1993.

Year	No. nests ^a	No. obs. days	Mean (\pm SD) nest survival rate			
			Daily survival rate by nest stage		Overall survival rate (egg-laying through nesting)	
			Egg laying and incubation	Nestling	Cowbird eggs/young ^b	Vireo eggs/young ^b
1990	8	83.0	0.917 \pm 0.036	— ^c	— ^c	— ^c
1991	36	418.5	0.921 \pm 0.015	0.956 \pm 0.022	0.190 \pm 0.070	0.171 \pm 0.062
1993	65	731.0	0.925 \pm 0.011	0.925 \pm 0.019	0.132 \pm 0.042	0.108 \pm 0.035
Combined	109	1,232.5	0.923 \pm 0.009	0.940 \pm 0.014	0.158 \pm 0.036	0.126 \pm 0.030

^a Includes nests observed for at least one day during egg-laying to fledging. Sample includes the 98 active nests found before egg-laying and an additional 11 found later in nesting. Not all nests were observed during both periods.

^b Cowbird incubation = 11.5 days and nesting period = 13 days. Vireo incubation = 15 days and nesting period = 12 days.

^c Insufficient data.

$P = 0.28$), among years ($\chi^2 = 0.1$), or among study areas in the same year (1991: $\chi^2_1 = 1.1$; 1993: $\chi^2_3 = 0.0$), so data were pooled for analysis.

The probability that a nest was successful was not related to the frequency of visits to the nest, regardless of the type of visit (Wilcoxon's signed-ranks test, median number of visits per day to: successful nests = 0.46 [$n = 14$]; depredated nests = 0.47 ($n = 84$); for all visits: $t_s = -1.45$, $P = 0.15$; "flushed" visits: $t_s = -0.83$, $P = 0.41$; "handled" visits: $t_s = -0.98$, $P = 0.33$). Among my study population, six nests were built that I was never able to locate. The behavior of the birds indicated that all of these nests failed, and the total nest life (initiation of building to failure) was no different for found (17.2 days, $n = 133$) and unfound nests (16.7, $n = 6$). Although it would be unreasonable to expect that human visitation to nests would have no impact on their survival rates, these data suggest that the effect of visits was small.

Approximately 16% of active vireo nests on

the study areas were successful (fledged vireo or cowbird young; Table 5). The average active life of Puerto Rican Vireo nests did not vary between parasitized and unparasitized nests (parasitized: 12.7 \pm 8.8 days, $n = 59$ because outcomes of 5 parasitized nests were unknown; unparasitized: 10.8 \pm 9.0 days, $n = 14$; median test $\chi^2_1 = 0.01$, $P = 0.94$). Furthermore, parasitism did not significantly influence the outcome (success or failure) of a nest (Table 5; $\chi^2_1 = 0.15$, $P = 0.70$).

CAUSES OF NEST FAILURE

In the following section, unless otherwise indicated, the sample included 133 nests which were found before or on the first day of egg-laying and for which the outcome was known.

Predation. Predation was the most significant cause of nest loss on the study sites. Approximately 70% of all nest attempts ended in predation, or 81% of all active nests. In 80% of predation events, the nest itself was undisturbed, suggesting an avian or reptilian predator. The most serious avian predator on both eggs and

TABLE 5. Nest fates of active Puerto Rican Vireo nests, Guánica Forest, Puerto Rico, 1990–1993. Data are from all years and study areas combined.

Nest fate	Percent of nests (n^a) related to parasitism status and nest fate			
	Parasitized (59)	Unparasitized (14)	Unknown (25)	Totals (98)
Abandoned during egg-laying	1.7 (1)	7.1 (1)	20.0 (5)	7.1 (7)
Abandoned during incubation	5.1 (3)	0.0 (0)	4.0 (1)	4.1 (4)
Predation on nest	69.5 (41)	71.4 (10)	72.0 (18)	68.4 (67)
Predation on adult	1.7 (1)	7.1 (1)	4.0 (1)	3.1 (3)
Hatching failure	3.4 (2)	0.0 (0)	0.0 (0)	2.0 (2)
Successful-fledged vireo	5.1 (3)	14.3 (2)	0.0 (0)	5.1 (5)
Successful-fledged cowbird	13.6 (8)	—	0.0 (0)	8.2 (8)

^a Includes only nests found on or before egg-laying, which received at least one host egg, and for which final outcome was known. Nests under "parasitized" and "unparasitized" had to meet the criteria described in the Methods section.

TABLE 6. Season-long reproductive success of female Puerto Rican Vireos, Guánica Forest, Puerto Rico, 1991 and 1993. Averages are based on 6 females in 1991 and 17 females in 1993.

Component	Year			
	1991		1993	
	Mean \pm SD	Range	Mean \pm SD	Range
No. nest attempts/female	4.30 \pm 0.52	4–5	3.20 \pm 1.30	2–6
No. active nests/female	3.50 \pm 0.55	3–4	2.80 \pm 1.25	1–6
No. successful nests/female	0.67 \pm 0.82	0–2	0.41 \pm 0.52	0–1
No. vireos fledged/female	1.33 \pm 1.97	0–5	0.24 \pm 0.75	0–3
No. cowbirds fledged/female	0.00 ^a		0.35 \pm 0.49	0–1

^a Some Puerto Rican Vireo nests fledged cowbird young in 1991, but season-long reproductive success was not available for those females.

nestlings in Guánica Forest is probably the Pearly-eyed Thrasher (*Margarops fuscatus*) (W. Arendt, pers. comm.). Puerto Rican Lizard-Cuckoos (*Saurothera vieilloti*), Mangrove Cuckoos (*Coccyzus minor*), and Red-legged Thrushes (*Turdus plumbeus*) also may take eggs and nestlings (Rivera-Milán 1996). Black-whiskered Vireos (*V. altiloquus*) have been recorded puncturing and tossing eggs from nests in Puerto Rico (J. Wiley, pers. comm.), including one PRVI nest in this study (Woodworth, unpubl. data), raising the possibility of interference competition between congeners in this system. Cowbirds may act as nest predators (Arcese et al. 1996), and six potential cases of cowbird nest destruction were identified in this study, where nearly the entire contents of an undisturbed nest were found punctured or broken and uneaten beneath the nest; however, in the absence of direct evidence, these events were attributed to avian predation. A snake (*Alsophis portoricensis*) may take eggs, but this species is rare in Guánica. Approximately 20% of depredated nests were torn up, and were probably destroyed by mammalian predators, all of which are exotic in Guánica: rats (Wiley 1985, Rivera-Milán 1996) and, for low nests, mongooses and feral cats (Woodworth, pers. observ.).

Two nests were lost to predation on an incubating female (remains found on or beneath the nest). In one case the nest was destroyed along with the female; in a second, the unharmed nest was thereafter abandoned by the male.

Abandonment. Of 133 nests, 25 (19%) were never completed ("fragments," Nolan 1978). Known or suspected causes for abandonment were: the male was unmated ($n = 4$), the two members of the pair were building in two locations, one of which was eventually abandoned ($n = 6$), cowbird disturbance ($n = 2$), end of

season or onset of molt ($n = 2$), and unknown ($n = 11$). There were an additional 12 nests (9%) which were finished but in which no eggs were laid to my knowledge. Potential causes were the end of season or onset of molt ($n = 3$), cowbird disturbance ($n = 3$), and unknown ($n = 6$). Other passerines have been reported to build a high proportion of incomplete nests, e.g., Bell's Vireo, *V. bellii*, 21% (Barlow 1962), Prairie Warbler, 23% (Nolan 1978), and Yellow-hooded Blackbirds, 41% (Wiley and Wiley 1980).

Abandonment of active nests occurred 11 times (8%). Seven nests were abandoned during egg-laying (suspected causes: 6 cases of cowbird disturbance or partial clutch loss, 1 unknown) and four during early incubation (suspected: 3 cases of cowbird disturbance or partial clutch loss, and 1 human disturbance).

Hatching failure. Two parasitized nests were incubated for an extended period (21 and 27 days) but neither vireo nor cowbird eggs hatched. The two nests were of the same male in two different years. Nest watches and regular observations failed to show any abnormality in the pairs' nest attentiveness (Woodworth, unpubl. data).

Collapsed nests. Puerto Rican Vireo nests are thin-walled and appear fragile. However, they were strong enough to hold a brood of three vireo chicks (approx. 35 g on day 8), and nests containing vireo chicks were never known to collapse ($n = 9$ broods between 12 and 35 g). However, 32% ($n = 19$) of nests containing cowbird chicks of comparable weight collapsed, and median weight at collapse was just 19.3 g (range 12–25 g).

SEASON-LONG FECUNDITY

Females attempted at least two, and as many as six, nests in a single year (Table 6). Not all of

these nests received host eggs; females typically abandoned one nest each year before it became active. Pairs that lost a nest to a predator or other causes usually began building a new nest the following morning. The mean interval length from failure of one nest to initiation of the next clutch was 9.4 ± 2.5 days (range 7–18, $n = 26$ nests for which interval length was known to within one day). When the next nest was abandoned pre-laying, interclutch interval averaged 16.9 ± 7.6 days (range 11–28, $n = 3$). The length of the interclutch interval did not vary depending on the time of year (Kruskal-Wallis ANOVA on five 15-day periods, $\chi^2_4 = 6.23$, $P = 0.18$), the number of nest attempts previously made by a pair (0, 1, 2, 3, or 4 or more; Kruskal-Wallis ANOVA, $\chi^2_4 = 5.39$, $P = 0.14$), or the stage of the breeding cycle when the nest failed (defined as the number of days since egg-laying; $r_s = -0.16$, $t = -0.82$, $P > 0.05$).

Pairs which fledged young before about 10 June attempted to raise a second brood ($n = 6$). However, pairs which fledged young later in the season did not usually attempt another nesting; of 10 late-fledging (after 10 June) broods, only 1 pair began another nest, and their chick had died shortly after fledging. Two pairs which fledged 1 cowbird each began building the subsequent nest 10.5 and 13 days after fledging young from the first nest, whereas one pair that fledged 3 vireo chicks began the subsequent nest 14.5 days later.

Although average seasonal fecundity was markedly different between the two years studied (Table 6), the difference was not significant (t -test on square-root transformed data, $t_{5,9}$ (unequal variances) = 0.17, $P = 0.18$; however, the power of the test was low). Nest survival rates were not different between the two years (Table 3). Rather, three factors appeared to contribute to higher seasonal fecundity in 1991 than 1993: (1) a longer breeding season, (2) lower parasitism rates of 5 nests initiated in April of 1991 (from which a total of 5 vireo young fledged), and (3) cowbird eggs failed to hatch in 3 nests in 1991 (from which an additional 5 vireo young fledged).

DISCUSSION

The most significant causes of reproductive failure in this population of a tropical resident passerine were nest predation by native and exotic predators, and nest parasitism by the introduced

Shiny Cowbird. Predation and parasitism also are the most important causes of nest loss in north temperate songbirds (Martin 1992).

NEST SUCCESS

Daily nest survival of Puerto Rican Vireos on the four study areas was remarkably low, about 0.93 for eggs and nestlings combined. These rates are similar to those found for ten temperate species in a highly-fragmented landscape in Illinois ($\bar{x} = 0.938$, range 0.909–0.972; Robinson 1992) which are thought to represent sink populations (wherein local reproduction is not sufficient to balance mortality, and the populations persist through immigration from other areas). Predation was by far the most significant cause of nest failures, causing the demise of 70% of all nest attempts, or 81% of active nests. Shrub-nesting species (such as the PRVI in Guánica) may be particularly vulnerable to nest predation, as has been shown in North American songbirds (Martin 1992, 1993). Zenaida Doves (*Zenaida aurita*) in Guánica Forest also lost a large proportion of nests to predators (80% of nest failures), although overall nest survival was higher (0.973 ± 0.008 , $n = 42$, 1987–1992; Rivera-Milán 1996).

FREQUENCY, TIMING, AND IMPACT OF PARASITISM

Parasitism rates on Puerto Rican Vireos were approximately 73–83% throughout the study, higher than that recorded in open habitats in interior Puerto Rico 10 years earlier (36.3%, 1976–1984, $n = 11$; Pérez-Rivera 1986; but note different empirical methods and habitat). High rates of parasitism have been observed on other Shiny Cowbird hosts, including the Rufous-collared Sparrow, 72.5% (Fraga 1978), Chalk-browed Mockingbird, 76.9–86.2% (Fraga 1985), Yellow-shouldered Blackbird, nearly 100% (Post and Wiley 1977a, Post et al. 1990), > 75% on 6 species in southwestern Puerto Rico (Wiley 1985), and the Black-whiskered Vireo, 73–88% (Post et al. 1990). The average number of cowbird eggs laid in parasitized Puerto Rican Vireo nests (1.4) was similar to that found in many other hosts in other regions of Puerto Rico and the Caribbean (Post et al. 1990), with the exception of the Yellow-shouldered Blackbird (3.0 cowbird eggs per parasitized nest, Post and Wiley 1977a). Yellow-shouldered Blackbirds are widely considered to be preferred hosts of the

cowbird in Puerto Rico, but do not breed in Guánica Forest.

Parasitism had a large negative effect on vireo reproductive success, reducing by 82% the number of host young fledged per active nest. As in other small vireos (e.g., Solitary Vireo, *V. solitarius*, Marvil and Cruz 1989; Black-capped Vireo, Grzybowski 1995), cowbird parasitism decreased hatching success and caused starvation of host young in the nest. This effect is typical when there is a shorter incubation period for parasitic eggs than host eggs, and parasites are much larger than the host (Friedmann 1963, Rothstein 1975a).

Cowbirds may act to further decrease host reproductive success by removing eggs or nestlings of nests they did not parasitize, thereby causing the host pair to renest and generating additional breeding opportunities for the cowbird (Arcese et al. 1996). The extent to which this occurs has not been well-documented with direct evidence in any system. Unfortunately, punctured eggs may be attributable to a variety of agents, including avian predators (Manolis 1982), conspecifics (Pribil and Picman 1991), congenics (this study), or laying cowbirds (Post and Wiley 1977a, Scott et al. 1992). The question presents an important problem for further research, for if cowbirds are in fact important agents of nest failure, then they have an even greater impact on host demography than previously appreciated (Arcese et al. 1996).

Limited data suggested that nests initiated in April may be less likely to be parasitized than nests initiated later in the season. Such an effect may occur if cowbird and host breeding periods do not overlap completely. Consistent with this, the breeding season of the cowbird is reported to peak in June in southwestern Puerto Rico (Wiley 1985) and in May to October in its native Trinidad and Tobago (Manolis 1982). Conversely, such an effect might be seen if cowbirds are "saturated" early in the season due to synchrony of first host nests (e.g., Wiley and Wiley 1980). The seasonal nature of the dry forest led to all PRVIs laying their first clutches within a two-week period; however, if saturation were the mechanism responsible for the lowered parasitism rate in April 1991, it also would have led to decreased parasitism in May 1993, and this was not observed.

The possibility that parasitism rates are lower early in the season is important because it im-

plies that early-nesting pairs may escape parasitism and successfully rear vireo young. From an evolutionary standpoint, this is of interest because it would select for earlier breeding by the vireo as a defense against parasitism. From a population dynamics standpoint, the resulting reproduction might produce enough young to compensate for lowered success during the remainder of the season. These topics are treated in more detail later in the discussion.

BEHAVIORAL DEFENSES AGAINST PARASITISM

Despite the high impact of parasitism in this system, Puerto Rican Vireos do not appear to have behavioral defenses against parasitism. Wiley (1985) found that four of five host species in nearby Boquerón Forest also did not desert in response to parasitism (Yellow Warblers *Dendroica petechia* were the exception). Because the Shiny Cowbird only has been in southwestern Puerto Rico for about 35 years, this result is not unexpected; presumably, insufficient time has elapsed for an ejection response to evolve ("evolutionary lag," Rothstein 1975b). However, even given appropriate time, Puerto Rican Vireos might not be expected to evolve defenses. First, Puerto Rican Vireos have small bills, so grasp ejection is probably not an option for them (Rothstein 1975a, Rohwer and Spaw 1988). Puncture-ejection may be costly, because cowbird eggs are relatively thick-shelled (Spaw and Rohwer 1987), and a host attempting to puncture a cowbird egg may risk damaging its own egg (Rothstein 1975a, Rohwer et al. 1989). Thus, although cowbird parasitism is costly in terms of reproductive success, egg ejection may not evolve. Black-capped Vireos and Bell's Vireos (also in the *V. griseus* subgroup) are among the small-billed acceptors for whom Rohwer and Spaw (1988) make this argument.

An alternative defense available to small-billed hosts is to abandon parasitized nest attempts (reviewed in Rothstein 1990). Puerto Rican Vireos did not abandon parasitized nests with any greater frequency than they did unparasitized nests. Although they may desert in response to harassment by cowbirds or egg-removal, such a response is probably a generalized antipredator response, rather than one specifically aimed at preventing parasitism (Rothstein 1975a). The high incidence of nest abandonment after egg-removal in this study is consistent with

the results of Hill and Sealy (1994), who found that Clay-colored Sparrows (*Spizella pallida*) that abandoned parasitized nests did so in response to egg removal associated with parasitism, rather than to addition of the parasitic egg *per se*.

Sunrise nest attentiveness also may influence abandonment behavior. Puerto Rican Vireos did not spend the night on the nest during egg-laying (Woodworth, unpubl. data) and so are unlikely to be present on the nest in the pre-dawn hours when cowbirds come to lay (Neudorf and Sealy 1994). Although sunrise nest attentiveness by itself is apparently not effective in preventing parasitism, especially in small hosts (discussed in Neudorf and Sealy 1994), birds which are present during the cowbird visit might be more likely to abandon in response to parasitism (Burhans 1996).

Whether or not parasitism will exert a selective force for abandonment will depend on parasitism rate, predation rate, time of season, and stage of the nest when parasitized. Using Pease and Grzybowski's (1995) model of seasonal fecundity, Woodworth (1995) predicted that abandonment would be advantageous for Puerto Rican Vireo females in Guánica only if parasitism rates were below about 0.25 cowbird eggs laid per susceptible nest per day, or 82%, close to that actually observed. If parasitism rates in nature varied around this threshold parasitism rate, the direction of selection pressure also would vary, effectively preventing the evolution of a consistent behavioral response.

TIMING AND LENGTH OF THE BREEDING SEASON

The onset of breeding was apparently triggered by rainfall. Guánica Forest is a highly seasonal tropical system—almost no rain falls from December to March, and the forest loses up to 50% of its leaf area in the winter (Murphy and Lugo 1986). Arthropod levels peak in the wet season in the Neotropics (Poulin et al. 1992). Thus, the arrival of the rains may act as a proximate cue for the onset of breeding in Puerto Rican Vireos. Such a relationship has been shown for other tropical landbirds breeding in arid or variable environments (Marchant 1960, Fogden 1972, Young 1994), and for columbids in Puerto Rico (Rivera-Milán 1996). The association between the onset of the rains and the initiation of the breeding season suggests that PRVIs are already

breeding at the first available opportunity. Thus, the vireos would be unable to evolve earlier breeding as a defense against parasitism (discussed above).

Puerto Rican Vireos stop breeding by July or August, and do not breed during the second, larger peak of rainfall in September–November. Possible ultimate factors include the need to accomplish post-breeding molt before the “lean season” (Fogden 1972) or before migrant birds arrive (Faaborg et al. 1984). Additionally, if survival rates of late-fledging chicks are poor, selection may act to limit late-season reproduction (discussed in Faaborg et al. 1984). Young (1994) found that reproduction in tropical House Wrens (*Troglodytes aedon*) was generally timed so that post-breeding activities such as molt and dispersal of young coincided with the peak in arthropod abundance.

The breeding seasons of birds in Guánica is relatively restricted compared to birds in other tropical areas. Based on local rainfall data and the observed relationship between rainfall and breeding, I estimated that Puerto Rican Vireo breeding seasons from 1984–1994 varied from 69 to 112 days, averaging 97 (Woodworth 1995). The shortest seasons are about equal to those reported for temperate species (Nice 1937, Ricklefs 1969, Nolan 1978), and the longest are comparable to those reported for arid tropical environments in Ecuador (Marchant 1960). From the initiation of nest-building onward, a complete reproductive cycle (from nest-building through post-fledging care) requires about 50 days, and so PRVIs could successfully raise at most only 2–3 broods per season. However, the breeding season of Puerto Rican Vireos in other areas of Puerto Rico may not be so constrained. In 1993 for example, when breeding in Guánica was delayed until May because of drought, Puerto Rican Vireos in a moist forest reserve were breeding in April (R. Pérez-Rivera, pers. comm.).

IMPLICATIONS FOR PERSISTENCE OF THE PUERTO RICAN VIREO

Puerto Rican Vireos are relatively long-lived, with annual survival rates of 68 to 74%, depending upon the sample used (Faaborg and Arendt 1995, Woodworth 1995, respectively). Nonetheless, the high parasitism rates, large negative impact of parasitism on reproductive output, and high predation rates suggest that re-

productive success may not be sufficient to balance mortality in this population, regardless of the species' relatively high survival rate. A population dynamics analysis of Puerto Rican Vireos in Guánica (Woodworth 1995) showed that despite the high predation rates, the population would be capable of producing enough young to balance mortality if the cowbird was absent from the system. The invasion of the cowbird, however, has lowered productivity below that needed to replace adult losses. These conclusions were robust to a wide range of variation in adult survival, juvenile survival, nest failure rate, parasitism rate, and breeding season length. Furthermore, even a complete lack of parasitism early in the season did not allow the modeled population's season-long production to equal mortality.

The fairly restricted breeding season, in combination with a small clutch size, means that PRVIs have a relatively low reproductive potential. Reproductive potential is an important predictor of a population's "resilience" (its ability to recover from perturbation, Pimm 1991). Therefore, if PRVIs were reduced to low numbers, their recovery to former levels might require a prolonged period, with all of the demographic risks associated with small population size. Furthermore, PRVIs have a low rate of dispersal and typically disperse short distances (Woodworth et al., in press), and so Guánica Forest may be effectively an "island" of habitat sandwiched between the coast and inland agricultural and residential areas. Fragmentation of habitat by dispersal barriers may predispose populations to extinction (Diamond 1985). For these reasons, the future existence of the PRVI as a breeding bird in Guánica Forest is in doubt.

The persistence of the PRVI in other parts of Puerto Rico will depend on the distribution and abundance of the cowbird, parasitism and predation rates in other habitats, dispersal rates and distances, and habitat fragmentation. Understanding the mechanisms by which PRVI populations persist, or decline, in the face of high parasitism rates by the introduced cowbird is of fundamental importance to designing effective conservation strategies. The Antilles are home to many new hosts of the cowbird, and only by understanding these interactions will we be able to protect the Puerto Rican Vireo and other endemic songbirds of the region.

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