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BREEDING BEHAVIOR OF THE PLUMBEOUS VIREO IN NEW MEXICO

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ABSTRACT.—The Plumbeous Vireo (*Vireo plumbeus*) is a poorly studied songbird species that breeds within the interior western United States and Mexico. We studied the breeding behavior of Plumbeous Vireos within pinyon-juniper habitats in northeastern New Mexico in 1996 and 1997. Over both years we located and monitored 40 nests and conducted behavioral observations throughout the nesting cycle. From these observations we described and compared basic behavioral traits of male and female vireos during their nest-building, egg-laying, incubation, and nestling stages, and their response to potential predators near the nest. Male vireos displayed potential nest sites to females, but the females selected the site to be used and built most of the nest. Vireos often did not initiate egg-laying until 2–3 d after nest completion. The female tended to incubate eggs and brood nestlings more than the male, but both parents contributed equally in provisioning the young. Brown-headed Cowbirds (*Molothrus ater*) parasitized 77% of nests in 1996, 63% in 1997, and parasitism was the primary cause of nest failure in this population. The conspicuousness of vireos around the nest, particularly during the nest-building stage, may contribute to high parasitism levels. Vireo aggression near the nest may also act as a cue to help cowbirds locate nests.

Key words: Plumbeous Vireo, *Vireo plumbeus*, breeding behavior, brood parasitism, egg-laying, incubation, nesting cycle, nest-building, Solitary Vireo.

The Plumbeous Vireo (*Vireo plumbeus*) is a small (15–20 g), migratory songbird that breeds in the mountainous regions of the interior western United States and western Mexico and winters primarily in western Mexico (Curson and Goguen 1998). On its breeding grounds the Plumbeous Vireo resides mainly within conifer-dominated forests (Curson and Goguen 1998), and like many vireo species, it appears quite susceptible to brood parasitism by the Brown-headed Cowbird (*Molothrus ater*; Goguen and Mathews 1998, Ortega 1998, Chace et al. 2000). Although current population trends of the Plumbeous Vireo appear stable (Peterjohn et al. 1995), the prominence of cowbird parasitism in most populations that have been studied, and the large reductions in nesting success that result from it, have raised concern over whether this species may be at risk over large areas of its range (Marvil and Cruz 1989, Goguen and Mathews 1998).

Most aspects of Plumbeous Vireo ecology and behavior are relatively unknown. This is partly due to a paucity of research in the interior West. The prior subspecific status of the Plumbeous Vireo (formerly *Vireo solitarius plumbeus*) within the former Solitary Vireo

complex may also have limited research interest before its recent split and attainment of full species status (Johnson 1995, American Ornithologists' Union 1997). We studied Plumbeous Vireo breeding behavior in pinyon-juniper habitats of northeastern New Mexico in 1996 and 1997. At our study site this species breeds regularly within pinyon-juniper and mixed-conifer habitats and occasionally in riparian habitats (Goguen et al. 1998). It is also a common host of the Brown-headed Cowbird, experiencing parasitism in >85% of its nests in pinyon-juniper habitats in some years (Goguen and Mathews 1998). Our objective is to describe aspects of the breeding biology and behavior of this understudied species. Information gained from this research will provide basic life history data and insight into how vireo behavior influences rates of nest predation and brood parasitism.

METHODS

Study Site

We conducted our research on the National Rifle Association Whittington Center (WC) and the adjacent V-7 Ranch (V7R) in Colfax

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County, northeastern New Mexico. The 13,350-ha WC, a National Rifle Association-affiliated shooting facility that remains mostly undeveloped, is ungrazed by livestock during the songbird breeding season. The 8090-ha V7R is an active cattle ranch that uses a seasonal grazing system at a moderate stocking rate (~45% annual forage use). Both sites lie along the eastern edge of the foothills of the Sangre de Cristo Mountains at the interface of shortgrass prairie and coniferous forest habitats.

We studied vireos on 8 previously established 35-ha plots within pinyon-juniper habitat (Goguen and Mathews 1998). Pinyon-juniper habitat lies in a narrow band on the lower slopes of the foothills (~1990–2130 m) between shortgrass prairie at lower elevations and mixed-conifer forests of ponderosa pine (*Pinus ponderosa*; plant names follow Stubbendieck et al. 1997) and Douglas-fir (*Pseudotsuga menziesii*) at higher elevations. Pinyon-juniper is an open woodland habitat dominated by pinyon pine (*Pinus edulis*), with one-seed juniper (*Juniperus monosperma*) scattered throughout. Woody understory consists of oaks (*Quercus spp.*), alder-leaf mountain mahogany (*Cercocarpus montanus*), and skunkbrush sumac (*Rhus aromatica*). Herbaceous understory is generally sparse, but intrusions of shortgrass prairie dominated by blue grama (*Bouteloua gracilis*) are common, particularly at the lower edge of the habitat.

Over 35 bird species regularly breed in the pinyon-juniper woodlands (Goguen and Mathews 1998). Among the most common breeding species are Spotted Towhee (*Pipilo maculatus*), Chipping Sparrow (*Spizella passerina*), Bushtit (*Psaltriparus minimus*), Blue-gray Gnatcatcher (*Poliptila caerulea*), Western Wood-pewee (*Contopus sordidulus*), and Western Scrub-jay (*Aphelocoma californica*). The Brown-headed Cowbird is also common and heavily parasitizes several songbird species (Goguen and Mathews 1998). The Plumbeous Vireo, a regular breeder, is found in relatively low densities in this habitat (Goguen and Mathews 1998).

Research Methods and Analyses

We observed Plumbeous Vireo nests in pinyon-juniper habitats from May to July 1996 and 1997 as part of a study monitoring the nesting success of pinyon-juniper songbird communities. Each year nests were located

and monitored on, and in habitat surrounding, the study plots. We visited plots every other day to monitor nest fates and located nests by observing adult behavior. This allowed us to locate most nests (65%) in the nest-building or egg-laying stages. We checked all nests with extendable poles with mirrors to monitor nest contents and fate, and to determine parasitism status. Nests were considered successful if they fledged at least 1 vireo young. Nests were considered failed due to cowbird parasitism if they were abandoned within 3 d of the appearance of a cowbird egg or if the presence of a cowbird nestling led to the death of all vireo young.

By conducting intensive behavioral observations at a subset of vireo nests each year, we measured vireo behaviors throughout the nesting cycle. We divided the nesting cycle into 4 general periods: (1) Nest-building period began with the placement of the 1st piece of nesting material and continued until the 1st egg was laid; (2) egg-laying period started the morning the 1st egg was laid and continued until the last egg was laid; (3) incubation period started the morning of clutch completion and continued until the 1st egg hatched; and (4) nestling period ran from the day the 1st egg hatched to the day the last nestling fledged.

We observed vireo behavior from 10–15 m away from the nest in 60-min observations. All observations began after a 10-min buffer period to allow the birds to acclimate to our presence. Many nests were observed more than once in a stage (61% of nests) and/or in more than 1 stage (57% of nests), but never twice on the same day. We used the individual breeding pair as the unit in analyses. Behavioral measures obtained from repeat observations of the same nest during the same nesting interval were averaged, and only mean values were used.

During observations, we measured the following behaviors: (1) time spent on the nest by each sex; (2) total time nest was attended within 5 m, including on the nest, by at least 1 adult; (3) overall number of visits to the nest by the male and female (estimate of the amount of activity near the nest); (4) number of trips to the nest with nesting material or food; (5) number of “chatter” calls (a call consisting of a series of loud, harsh notes used by both sexes; Curson and Goguen 1998) by sex;

and (6) time spent singing by the male. Sexes were distinguished by song; only the male uses the primary song (Curson and Goguen 1998). We maintained additional notes on intraspecific behavior and recorded descriptions of encounters with predators or cowbirds. Upon completion of an observation, we checked nest contents and immediately departed from the nest site.

Using a modified Mayfield method (Heisey and Fuller 1985), we calculated nesting success and cause-specific failure rates of Plumbeous Vireo nests by year and nesting stage. Because of concerns of normality and large differences in variances, we made comparisons of behavioral variables within, and among, nesting stages using nonparametric tests (Sokal and Rohlf 1981). Differences were considered statistically significant if $P < 0.05$. Because of small sample sizes and low statistical power of tests, however, we also discuss trends in data when results approached significance ($P = 0.10$ to 0.05).

RESULTS AND DISCUSSION

We located and monitored 20 vireo nests in 1996 and 20 nests in 1997. Because of inaccessibility or late discovery, we were unable to determine parasitism status for 4 of these nests. We conducted behavioral observations at 14 nests for 72 h in 1996 and 9 nests for 17 h in 1997 for a total of 89 h of observation.

Vireo Nesting Behavior

VIREO ARRIVAL AND TERRITORY ESTABLISHMENT.—Male Plumbeous Vireos arrived before females, generally in early May (Curson 1996). Males were often observed building “bachelor nests” prior to pairing. Bachelor nests are loosely constructed structures that resemble a shallow hammock. Often more than 1 bachelor nest was built and attended simultaneously. One male built at least 5 bachelor nests across the summer. Other closely related vireo species are also known to build bachelor nests (Blue-headed Vireo [*Vireo solitarius*], James 1978; White-eyed Vireo [*V. griseus*], Hopp et al. 1995; Gray Vireo [*V. vicinior*], J. Barlow personal communication). In the case of the formerly conspecific Blue-headed Vireo (Johnson 1995), bachelor nests appear to act as a place of display when the female arrives and may represent prospective nesting sites from which

the female selects (James 1978). In our research all bachelor nests were abandoned following pairing, and the significance of these nests remains unclear.

The interval between pair formation and nest initiation appeared to be short. In 1 case a male paired and started nest construction with a female during a 24-h period. In 2 other cases previously unpaired males were paired and nest-building when next observed approximately 48 h later. Nest-site selection involved both sexes. Males displayed prospective nest sites to females. In this display a singing male made repeated trips to a potential nest site, attaching materials such as insect or spider silk, while the female observed. Our brief observations did not allow us to determine the total number of sites displayed by each male, but in 2 cases we observed a male display at least 2 different sites to a female.

Although the male Plumbeous Vireo initially displays potential nest sites for the female, our observations suggest that ultimately the female selects the site to be used; males attach nest materials at >1 prospective site, but the female joins in building at only one. In many other vireo species (e.g., Bell's [*Vireo bellii*], Black-capped [*V. atricapillus*], Blue-headed, Hutton's [*V. huttoni*], Philadelphia [*V. philidelphicus*], and Yellow-throated [*V. flavifrons*]), males and females appear to exhibit roles similar to those observed for the Plumbeous Vireo during nest-site selection; males display prospective sites while females choose the site to be used (James 1978, Brown 1993, Davis 1995, Grzybowski 1995, Moskoff and Robinson 1996). For example, male Blue-headed and Yellow-throated Vireos display 1 or more potential sites, but the female chooses among them or may even select a different site (James 1978). The process of nest-site selection in Plumbeous Vireos deserves a more complete examination.

NEST-BUILDING STAGE.—We observed 12 pairs building their nests for a total of 24 h. Plumbeous Vireos build an open, semipensile cup nest often placed near the end of a low branch or in the outer foliage near the top of a tree (Curson 1996). The main nest structure generally requires 4–5 d to complete. Lining of the nest extends the stage 2–3 additional days. The longest nest-building period we observed took 10 d.

First nesting attempts started during the 2nd week of May. The male initiated the nest

as part of the nest-site selection display and initially avidly assisted the female in the nest-building process (Fig. 1). The male's contribution became minimal after 1 or 2 d, however. In constructing the nest the female often sat in the nest and rotated her breast against the nest walls to form the cup shape after attaching new nesting materials. Although the male rarely contributed nesting material, he accompanied the female during 76% of her trips to the nest ($n = 99$ trips). During these visits the male occasionally assisted in shaping the nest, but more often he simply perched close and sang. Only the female was observed constructing the nest's lining.

We often observed a hiatus between apparent completion of the nest and onset of egg-laying. Of 7 nests for which we have data, egg-laying was initiated with no pause in 2 cases, and with a 2- to 3-d pause in the other 5 cases. During the hiatus both adults visited the nest occasionally, but without new nesting materials. During the hiatus it was also common to observe either the male or female sitting quietly on an empty nest as if incubating. Of 6 observations conducted during the hiatus, females sat on the empty nest for at least 1 min during 2 observations, while males sat during 3 observations. In only the observations where adults were on the nest, females occupied the nest for an average of 11.5 min, while males averaged 20 min. During 1 observation, a male sat on an empty nest for 39 min. This male also sang from the nest for 2 min. Bent (1950) also reported an instance of a Plumbeous Vireo sitting on an empty nest.

Other vireo species are known to exhibit a brief (1–3 d) hiatus between nest completion and egg-laying (e.g., Bell's, Hutton's, and White-eyed Vireos; Brown 1973, Davis 1995, Hopp et al. 1995). The significance of this hiatus, and associated false incubation behavior for Plumbeous Vireos, is unclear. However, it may deceive cowbirds. Cowbirds generally parasitize nests during the host's egg-laying stage (Nolan 1978, Marvil and Cruz 1989) and may use the switch in host behavior from nest-building to longer bouts on the nest as a cue to assess when a host has begun laying its eggs. Plumbeous Vireo nests are parasitized prior to egg-laying more frequently than other hosts on our study site; 26% of 90 cowbird eggs were laid prior to vireo egg-laying, whereas other hosts examined received <10% of cow-

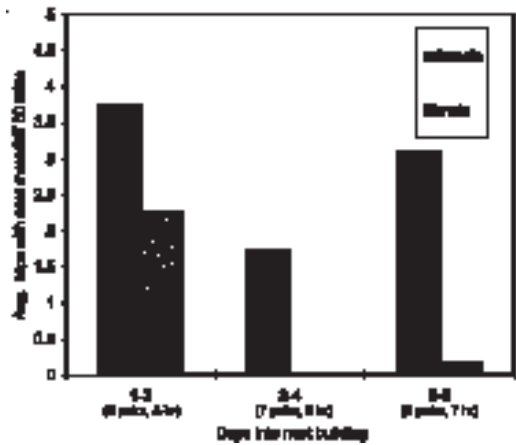


Fig. 1. Average number of trips with nesting material by Plumbeous Vireo pairs building nests in pinyon-juniper woodlands in New Mexico, 1996 and 1997. Delivery rate of nesting materials did not differ by sex during days 1–2 ($U = 41.5$, $P = 0.29$), but was higher for the female during days 3–4 ($U = 38.5$, $P = 0.02$) and days 5–9 ($U = 31.0$, $P = 0.03$).

bird eggs during this interval (Goguen 1999). Thus, this false incubation behavior may instigate early laying by cowbirds. Although Plumbeous Vireos typically accept cowbird eggs, of 23 cowbird eggs laid prior to vireo egg-laying, 30% were deserted with the nest and 9% were buried under the nest lining (Goguen 1999). These desertions are probably not a result of cowbird egg recognition by vireos, but rather they may represent a generalized response to an egg appearing in the nest at an inappropriate time (Rothstein 1975).

EGG-LAYING STAGE.—We observed 7 nests for a total of 11 h during the egg-laying stage. Females laid 1 egg per day. Among unparasitized vireo nests we observed 10 four-egg clutches and 1 three-egg clutch. Based on larger sample sizes, clutch sizes of Plumbeous Vireos are most commonly 4, occasionally 3, and rarely 5 (Chace et al. 2000). Thus, the egg-laying stage (i.e., the period from the morning of the 1st egg laid to the morning of the last egg) lasts from 2 to 4 d. The earliest vireo egg laid in 1996 was on 16 May, and the earliest in 1997 was 20 May. The peak of vireo clutch initiations in both years was in the last week of May to the 1st week of June.

Adult activity at the nest appeared to vary across the egg-laying stage (Table 1). Early in this stage adults tended to remain away from the nest for long periods. When an adult did

TABLE 1. Behavior during the egg-laying stage of Plumbeous Vireos nesting in pinyon-juniper woodlands in New Mexico, 1996 and 1997.

	Days into the egg-laying stage	
	1-2	3
Number of pairs observed	5	5
Number of 60-min observations	6	5
Minutes on nest by female ^a	19.6 (23.3)	29.3 (26.0)
Minutes on nest by male	11.2 (15.4)	18.7 (22.7)
Total minutes with an adult on nest	30.8 (20.7)	48.0 (21.7)
Visits to the nest by either adult	1.0 (1.7)	0.6 (0.55)
Total minutes nest unattended within 5 m by either adult	17.2 (18.8)	8.0 (17.9)

^aAll results reported as mean/60-min observation period (standard deviation). No means differed between days 1-2 and day 3 (Mann-Whitney U test, $P > 0.05$).

visit the nest, it usually remained only briefly, as though checking on the nest. Time on the nest tended to increase for both sexes in the last day of egg-laying (i.e., the day before the final egg was laid; Table 1). On day 3 the female was present on the nest for >60 min for 2 of 5 observations. Based on pre-sunrise nest checks, females did not roost on the nest at either of 2 nests observed on the 2nd morning of egg-laying; but at 2 different nests observed on the 3rd morning, females were present roosting in both cases (Curson unpublished data). These results suggest that incubation may begin the day prior to the laying of the last egg.

INCUBATION STAGE.—We observed 11 nests for a total of 33 h during the incubation stage. This included 4 nests with only vireo eggs and 7 nests that contained vireo and at least 1 cowbird egg. Estimates of the length of the incubation stage range from 14 to 15 d (Marvil and Cruz 1989, Curson and Goguen 1998). In parasitized nests, however, incubation of the cowbird egg takes about 11 d.

Both sexes took turns incubating the clutch, although the female tended to spend more time incubating than the male ($n = 11$ pairs, mean minutes on nest per hour $\pm s$; female = 34.7 ± 15.3 min h^{-1} , male = 21.1 ± 12.1 min h^{-1} ; Mann-Whitney U test, $U = 86.0$, $P = 0.09$). Female Plumbeous Vireos possess a full, vascularized ventral brood patch while males possess only a partial, nonvascularized patch (Curson and Goguen 1998). Adults generally replaced each other on the nest as incubation bouts were completed. Because of nearly constant incubating, the nest was attended almost continuously during this stage (Table 2). While incubating, females were silent and still, moving only rarely to rotate the eggs or shift position, and only vocalizing with chatter or con-

tact calls near the end of an incubation bout. Males were also usually silent but sang from the nest in 14 of 36 incubation bouts (38%). While 1 adult incubated, the non-incubating adult rarely remained close to the nest. In most cases the non-incubating adult disappeared from the nest vicinity. Although Willard (1908) reported a non-incubating adult frequently feeding an incubating adult on the nest, we did not observe males feeding incubating females, or vice versa.

We were able to observe many incubation switches between the male and female. The process generally involved fairly predictable patterns: Males moved about the territory while singing, occasionally approaching the vicinity of the nest. Near the time of a switch, the female uttered "chatter" or soft contact calls, presumably to signal the male. The male then slowly moved from branch to branch approaching the nest. When the male arrived, the female left either quietly or with soft contact calls, while the male quickly replaced her on the nest. Males did not always replace the female. On 4 occasions the male, rather than incubating, perched near the nest and sang. In 1 of these cases the male sang close to the nest for 32 min until the female returned and resumed incubating.

NESTLING STAGE.—We observed 12 nests for a total of 21 h during the nestling stage. Three of these nests had only cowbird nestlings, 8 had only vireos, and 1 had both cowbird and vireo nestlings. Most of our observations (20 h) took place at nests with nestlings that were <10 d old. The nestling stage lasts 13-16 d in unparasitized nests (Marvil and Cruz 1989, Curson and Goguen 1998). In parasitized nests in which the cowbird hatches first, the later-hatching vireo eggs rarely survive beyond a few days (Marvil and Cruz 1989), while the

TABLE 2. General behavioral characteristics based on nesting stage of Plumbeous Vireos nesting in pinyon-juniper woodlands in New Mexico, 1996 and 1997.

	Nesting stage			
	Nest-building	Egg-laying	Incubation	Nestling
Number of pairs observed	12	7	11	12
Number of 60-min observations	24	11	33	21
Total minutes nest attended (Adult on or within 5 m) ^a	19.0 (15.9)a	44.7 (20.2)b	58.7 (3.2)b	42.8 (17.2)b
Minutes adult on nest ^a	6.4 (7.0)a	38.2 (21.4)bc	55.8 (5.7)c	33.3 (20.6)b
Visits to the nest by female ^a	4.0 (3.6)a	0.5 (0.5)b	0.5 (0.5)b	1.6 (1.3)b
Visits to the nest by male	0.8 (1.6)	0.1 (0.4)	0.7 (0.8)	1.1 (1.2)
Chatter call, male (min)	0.3 (0.3)	0.3 (0.3)	0.9 (0.9)	2.1 (3.6)
Chatter call, female (min)	0.2 (0.3)	0.1 (0.1)	0.2 (0.4)	0.9 (2.3)
Singing (min)	14.1 (7.9)	10.6 (9.5)	21.6 (12.2)	13.4 (11.6)

^aAll results reported as mean/60-min (standard deviation). Based on Kruskal-Wallis tests, means were significantly different among nesting stages for total time nest attended ($H = 23.04$, 3 df, $P < 0.001$), total time adult on nest ($H = 23.60$, 3 df, $P < 0.001$), and visits to the nest by the female ($H = 13.80$, 3 df, $P = 0.003$). For these variables, values followed by differing letters are significantly different. For all other variables, means are not significantly different ($P > 0.05$).

TABLE 3. Adult brooding and food delivery rates during the nestling stage of Plumbeous Vireos nesting in pinyon-juniper woodlands in New Mexico, 1996 and 1997.

Age of young	Age of nestlings ^a		
	1-3 ($n = 8$ h)	4-6 ($n = 4$ h)	7-9 ($n = 8$ h)
Brooding (mean min on nest h ⁻¹ [s])			
Female	31.4 (25.3)	18.5 (21.1)	13.3 (21.0)
Male	13.5 (18.1)	15.4 (29.8)	4.1 (9.89)
Total ^b	44.9 (26.8)	33.9 (24.4)	17.4 (21.0)
Food delivery rate (mean feeding trips h ⁻¹ ([s])			
Female	0.6 (0.7)	1.0 (0.80)	1.6 (1.4)
Male	0.8 (1.0)	0.5 (0.6)	1.9 (2.1)
Total ^b	1.4 (1.5)	1.5 (1.3)	3.6 (2.3)

^aNumber of different pairs observed equals number of hours in all cases.

^bMean total brooding time and mean total feeding trips did not differ based on age groupings of nestlings (Kruskal-Wallis test, $P > 0.05$).

cowbird can fledge in only 10 or 11 d (Scott 1979).

During the nestling stage adults spent most time either brooding or searching for food for the nestlings. Both adults brooded the nestlings, but the female tended to brood more than the male (Table 3). Time spent brooding tended to decrease for both sexes as the nestlings matured (Table 3). During the initial 1-2 d, adults generally replaced each other on the nest as they delivered food, maintaining nearly constant brooding. During this period brooding bouts by the female sometimes exceeded 1 h. As the chicks matured, brooding became less frequent and by day 9 generally ceased during the daytime. This suggests that nestlings were capable of thermoregulation by this age.

Both adults contributed to feeding the young, but we found no evidence that either sex provided more food than the other (Table 3). Feeding rates increased as the chicks grew

older (Table 3). We did not have an adequate sample to evaluate the influence of nestling number on feeding rates, or to compare feeding rates at nests containing only a cowbird versus only vireo nestlings. Although a cowbird nestling probably receives more food than a similar-aged, but smaller, vireo nestling, a lone cowbird in a nest probably requires fewer food deliveries than a brood of vireo nestlings (e.g., Davison 1998).

Early in the nestling stage, nest switches by brooding adults took place in a manner similar to incubation switches described previously. Males sang from the nest during about half of observed brooding bouts (5 of 9 bouts), but usually only briefly (overall, males sang during 6.7% of 141.5 min on the nest). Both adults often foraged for food for nestlings within 10 m of the nest. When both adults were off the nest simultaneously, they often foraged together. Early in the nestling stage (before day 7), all

fecal sacs observed ($n = 4$) were consumed by adults. Later in this stage some fecal sacs ($n = 6$) were eaten (33.3%), but most were simply removed (66.7%). We obtained little information during the final days of the nestling stage and fledging.

Summary of Behaviors Through All Nesting Stages

Several general patterns existed across the nesting stages (Table 2). Visits to the nests were highest during nest-building and nestling stages as a result of regular delivery of nesting materials and food. Time on the nest was highest during incubation. Total time that an adult was present near the nest was also highest during incubation, but was consistently high during all stages in which eggs or young were present. Across all stages the female tended to spend more time on the nest than the male (Wilcoxin signed-ranks test, $z = -1.83$, $P = 0.07$). Singing rate did not differ among nesting stages. Chatter calling was observed rarely through most of the nesting cycle but appeared to be performed more commonly during the nestling stage. Chatter calls are believed to be used in longer-distance communication between males and females (Curson and Goguen 1998). Chatter calls may have been used most frequently in the nestling stage because of frequent approaches to the nest by feeding adults. Adults often called when approaching the nest with food, apparently to alert the other brooding adult. When adults were not brooding, chatter calls may also have been used to alert nestlings of an upcoming food delivery.

Vireo Nesting Success

Seventy-six percent of nests ($n = 17$) were parasitized in 1996 and 63% ($n = 19$) in 1997. These are among the highest recorded parasitism rates for this species, but they are lower than rates observed in previous years of research on this study site (1992–1995; mean = 86% parasitized; Goguen and Mathews 1998). Nests frequently contained more than 1 cowbird egg, averaging 2.15 cowbird eggs/parasitized nest in 1996, and 1.58 in 1997. Overall, of 25 parasitized nests across both years, 44% contained 1 cowbird egg, 36% contained 2, 12% contained 3, and 8% contained 4.

Parasitism during the nest-building stage led to the desertion of 3 nests prior to completion. Among nests that reached egg-laying,

nesting success was similar among years, and cowbird parasitism was the primary cause of nest failure (Table 4). Plumbeous Vireos rarely fledge their own young from nests that are parasitized during their egg-laying stage (Marvil and Cruz 1989, Goguen 1999). Cowbird eggs have a shorter incubation period and usually hatch about 3 d earlier than vireo eggs. The early hatching of the cowbird reduces vireo hatching success, and even if eggs hatch, the larger cowbird is able to outcompete the smaller young for food (Marvil and Cruz 1989). In this study parasitism led to nest failures during the egg-laying stage by causing desertions, probably due to clutch reduction by cowbirds, and, in 1 case, by removing all vireo eggs so that only 3 cowbird eggs remained. Most nest losses to parasitism resulted from starvation of vireo young during the nestling stage (Table 4). Across both years vireos averaged 2.36 vireo fledglings per unparasitized nest ($n = 11$) and 0.24 vireo and 0.44 cowbird fledglings per parasitized nest ($n = 25$). In 3 cases, 2 cowbirds were fledged from the same nest, but no mixed broods containing both vireo and cowbird young were fledged.

Nest predation was also a regular cause of failure (20.0% of parasitized and 18.2% of unparasitized nests were depredated), but probably had little overall impact on this heavily parasitized population. Plumbeous Vireos appear to be single-brooded in this population, but pairs that lost a nest to predation typically re-nested. These re-nesting attempts, however, were just as susceptible to parasitism as initial attempts because parasitism probabilities did not differ across the breeding season (Goguen 1999). Pairs that fledged a cowbird did not re-nest. Thus, pairs that raised cowbirds suffered total loss of reproductive potential for that year.

Response to Cowbirds and Predators

During our observations we witnessed several encounters between vireos and potential nest predators or cowbirds. Plumbeous Vireos exhibited different responses to a potential predator, depending on the specific circumstances of the encounter. When away from their nest, vireos joined other songbirds in mobbing potential threats. For example, we observed a pair of vireos join Western Wood-pewees in mobbing a cowbird. Close to their nest the

TABLE 4. Nesting success and cause-specific nest failure rates^a, by nesting stage, for Plumbeous Vireos nesting in pinyon-juniper woodlands in New Mexico, 1996 and 1997.

Year	Nesting stage			All stages
	Egg-laying	Incubation	Nestling	
1996 (<i>n</i> = 20)				
Successful (%)	72.3	74.6	54.0	29.1 ^b
Failed due to predation (%)	0.0	17.0	9.2	
Failed due to parasitism (%)	27.7	8.5	36.8	
1997 ^c (<i>n</i> = 20)				
Successful (%)	93.0	74.0	47.5	32.7
Failed due to predation (%)	0.0	13.0	17.5	
Failed due to parasitism (%)	7.0	6.5	35.0	

^aRates calculated using a modified Mayfield method described by Heisey and Fuller (1985).

^bSuccess rate across all stages calculated by multiplying proportion successful across the 3 nesting stages.

^cNest failures due to causes other than predation and parasitism accounted for an additional 6.5% during incubation stage in 1997.

response varied depending on whether an adult was on or off the nest. Usually if an adult was on the nest, and a potential predator approached, its initial response was to sink low into the nest until only its beak and tail protruded. We observed this behavior by vireos in response to a female cowbird, a Northern Mockingbird (*Mimus polyglottos*), and humans near the nest. The vireo usually remained on the nest in these encounters, unless the intruder approached closely, in which case the vireo flushed and attacked the intruder with swoops, strikes, and loud scolding calls, typically attracting its mate in the process.

Often when we approached the nest to check contents, both adults were off the nest. In these cases vireos initially flew near, chatter calling occasionally and changing perches frequently. As we neared the nest, the vireos became more agitated, using scolding calls and making closer flights. Once we were at the nest, vireos generally became extremely agitated, scolding constantly, and sometimes swooping. Responses to cowbirds or other small birds near the nest may be intense. We observed a vireo drive away a female cowbird that was apparently attacking its nestlings. A freeze-dried model of a female cowbird placed close to a vireo nest was usually viciously attacked with close swoops and bill strikes (Curson 1996). Often the vireos even perched on the model's back, repeatedly biting it on the head and neck.

For an avian brood parasite, the quality of a given host depends upon both the costs associated with locating and parasitizing its nests and benefits received in terms of parasite recruitment (Payne 1977). Cowbirds use host

behavior to locate nests (Norman and Robertson 1975, Thompson and Gottfried 1976), and Plumbeous Vireos were extremely conspicuous around the nest. Males often sang near or at the nest during nest-building and while on the nest in other stages. Both sexes frequently made long, direct flights to the nest when delivering nesting materials. Further, aggressive actions of this species may act as a cue for cowbirds to locate a nest (Smith 1981), while presenting little threat to the cowbird when laying (Curson 1996). Plumbeous Vireos accepted and often fledged cowbird eggs in our study (see also Marvel and Cruz 1989). Thus, our observations suggest that Plumbeous Vireos represent a high-quality host for cowbirds: nests are readily located and parasitized with little risk, and cowbird eggs are fledged at a high rate.

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