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BEHAVIOR AND NESTING BIOLOGY OF THE ST. ANDREW VIREO

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The St. Andrew Vireo (*Vireo caribaeus*) is a little known species endemic to the tiny Caribbean Island of San Andrés (12°35'N, 81°42'W), Colombia. Bond (1950) reported that this species was common there during his visit in 1948. In 1972, however, Barlow found it in any numbers only in brushy pastureland and mangrove swamp in the southern third of the island—an area of ca 17 km². Only brief notes on prebreeding weight and testes size (Russell et al. 1979), song in males (Barlow 1981), and on general status of the population (Bond 1950, 1974; Paulsen et al. 1969) have been published.

Herein we report for the first time the discovery and appearance of the nest, eggs, and nestlings of this vireo, and we comment briefly on parental care of nestlings, other nest-associated behavior, territoriality, vocalizations, foraging behavior, and interactions with other avian species. The observations presented here were made by Barlow in April 1972 and by Nash in June 1983.

METHODS AND STUDY SITE

Barlow visited San Andrés between 6-12 April 1972, in the company of S. M. Russell and D. W. Lamm. The party spent 2 days (10-11 April) on nearby Providencia Island (13°22'N, 81°23'W) (Russell et al. 1979). The principal study area on San Andrés was west of the Caribbean Hotel, 1.6 km south of the town of San Luis. Nash visited the same site between 3 and 8 June 1983.

The trip in 1972 involved acquisition of voucher specimens, tape recording of vocalizations, and a qualitative assessment of habitat, foraging behavior, nesting activity, and territoriality. Nash emphasized recording of vocalizations, and searched for evidence of nesting.

The color frontispiece is a painting by John P. O'Neill of a St. Andrew Vireo (Vireo caribaeus) at a nest.



Crude estimates of the size of territories were based on distances individual singing males traversed in response to playback of song, and the density of singing males in the primary study-site—an area of ca 50 ha immediately west of the hotel. Interactions with syntopic species were also noted.

San Andrés is ca 13 km by 4 km and, although generally low-lying, the island has a central ridge (elev. 95 m) running along much of its long axis. The indigenous population in 1983 exceeded 30,000 persons, most of whom lived in the northern two-thirds of the island. The town of San Andrés is the center of the tourist-oriented north end, and little habitat for scrub-dwelling birds remains in the town or nearby. Both of us were struck by the paucity of birds in the urban area during our separate visits.

Much of the island is covered with coconut palms (*Cocos nucifera*), planted in the 19th century. Isolated groves of native trees, some reaching 20 m, are associated with inland mangrove swamps.

The area in which we made our observations was shrubby pasture dotted with palms, mango (*Mangifera indica*), and dense patches of evergreen scrub as much as 30 m in diameter and 8 m tall. Several shallow pools were present in 1983, but a prolonged drought was underway in 1972 and a single spring was the only source of fresh water in the study area. Barlow traveled over much of the island by car in 1972, and in 1983 Nash wandered widely on foot in the southern third of the island in search of vireos.

Although our observations were largely anecdotal, some behavioral events were witnessed often enough to allow comparison with patterns in other species of the subgenus *Vireo*. It became apparent that we encountered different stages of the breeding cycle of *V. caribaeus* in our separate visits, and accordingly, the vireos responded differently to playback and resource availability in April than in June.

RESULTS AND DISCUSSION

Territorial behavior. — Territories were no more than 0.5 ha in area where V. caribaeus was common. On 7 April 1972, 10 males, seemingly uniformly spaced, were heard singing in the shrubby pasture-site in an area of about 5 ha. On other occasions (9 April 1972, 3 June 1983) four singing males, again equally spaced, occupied part of the same area.

Twice (both on 9 April 1972) three males sang within 5 m of one another, seemingly at territorial boundaries. Vocal dueling was taped only once in 1972 (9 April) but noted 20 times. In territorial encounters, males sang within a few meters of each other, and on all occasions but one they sang different songs. In that one instance, two of three males matched songs after a few minutes of singing different ones.

Response by males to playback of just-recorded song in April 1972 was sometimes accompanied by partial erection of feathers of the thorax and tail-fanning. In one example, reaction by a male to playback was intense with the feathers of the thorax ruffled, the tail broadly fanned, and wings held out slightly from the body. This aggressive display closely resembled high intensity postures seen in Bell's (*V. bellii*) and White-eyed (*V. griseus*) vireos in response to conspecific intruders (Barlow 1962).

Foraging behavior. – Vireo caribaeus is the most active and energetic of any of 20 foliage-gleaning species of vireos previously seen by Barlow (1980, pers. obs.) in the field. In fact, it reminded him more of a wood

warbler (Parulinae) or a kinglet (*Regulus* sp.) than had any other vireo. However, no special adaptations in jaw musculature for rapid gleaning were found in *V. caribaeus* by Orenstein and Barlow (1981) that might distinguish it from eight other species of generalized foliage-gleaning members of the subgenus *Vireo*.

Foraging occurred from as low as a few centimeters above the ground to 5 m in shrubby vegetation and occasionally as high as 10 m in tall trees. Arthropods were usually gleaned from leaves and twigs by stalking; hovering at a leaf cluster was seen only once in 30 min of continuous observation of a foraging bird in April 1972. On 5 June 1983, Nash saw a male catch a small (ca 2.5 cm) green caterpillar in its beak and then bang the caterpillar against a twig before eating it. Striking of prey against a twig is a foraging tactic frequently seen in many other vireos (Barlow, pers. obs.). Most prey items were too small to be identified. We saw no fruit eaten in several hours of general foraging observations.

Vireo caribaeus males sang frequently as they foraged. Males and females uttered single-note contact calls as they foraged. This habit of singing and calling while foraging is wide-spread among the Vireonidae (Barlow 1962, Barlow and James 1975, James 1976).

Comparisons with V. altiloquus.—Thicket-foraging vireos (subgenus Vireo) are regularly syntopic with arboreal-foraging species of the subgenus Vireosylva in the West Indies. On San Andrés the uncommon Black-whiskered Vireo (V. altiloquus canescens) occurs with V. caribaeus. These two vireos are separated by size (V. caribaeus, 10 g [N = 1] vs V. a. canescens, 21.9 g [N = 1]) and ecologically by height in the canopy at which they center their foraging activities. V. caribaeus frequented foliage below 5 m in contrast with V. a. canescens, which foraged higher—between 5 and 10 m (N = 1 male, 1 female, ca 40 min total observation time in April 1972). This Black-whiskered Vireo also differed from V. caribaeus in the high incidence (40% of all observations) of fruit consumed; in slow, deliberate foraging pace; and in frequency of occurrence of hovering at leaf clusters (in 20% of foraging attempts).

Vocalizations. — The song of V. caribaeus will be described in detail elsewhere, but may be heard on phonodisc (Barlow 1981). Song in this species is unusual in comparison with other vireos because it comprises three distinct patterns, each of which closely resembles the predominant song pattern in other species in the subgenus Vireo. The three patterns of singing by V. caribaeus are distinguished from each other by the kinds of syllables uttered in any given song bout. The structurally simplest of these is "chatter" song in which the same syllable is repeated from 2–20 (or more) times. This song format is shared with most populations of the Mangrove Vireo (V. pallens) of southern Mexico and northern Central America, the Cozumel Vireo (V. bairdi) of Cozumel Island, Mexico, and 268

the Thick-billed Vireo (V. crassirostris approximans) of Providencia Island ca 77 km to the north of San Andrés. The second type consists of songs of two different syllables, each of which may be uttered serially 1– 15 times. This pattern resembles that of the Jamaican White-eyed Vireo (V. modestus), and apparently also that of a population of the Mangrove Vireo (V. p. semiflavus) from Utila Island in the Bay of Honduras (Bond 1950). A second kind of polysyllabic song given by V. caribaeus, composed of three or more different syllables uttered in random order, is similar to the heterosyllabic song of all other "white-eyed" type vireos. All three of these song patterns are given by V. caribaeus in territorial contexts.

At least three calls have been identified in the repertoire of V. caribaeus including: (1) single notes uttered as adults forage together that are indistinguishable spectrographically from contact notes given by other "white-eyed" vireos; (2) a *chee chee*... heard in a variety of contexts in which agitation of some sort is evident, as when an observer is close to the nest; and (3) a "raspy-buzz" given in response to playback and emblematic of high intensity aggression. The last two calls resemble those of other "white-eyed" vireos (Barlow 1962). The paucity of calls described herein does not necessarily indicate a smaller repertoire of vocalizations by V. caribaeus in comparison to repertoire size of other "white-eyed" vireos, but rather that the call-note system has yet to receive adequate study.

After Barlow found no evidence of nesting activity and noted that three males had testes smaller than expected for full breeding condition (largest diameter 5 mm) in April 1972, it was assumed that breeding activities had not yet been initiated. Similarly in 1948 Bond (1950:48) saw no breeding activities in *V. caribaeus* in late April, leading him to predict that breeding in this species doubtless occurred in late May and early June during the first "rainy season" as with land birds in the Greater Antilles. In confirmation of this speculation, on 3 June 1983 Nash, attracted by the furtive behavior of a silent bird apparently paired with a singing male, discovered the first nest of *V. caribaeus* known to biologists. It was a pensile structure of typical vireonid construction (see Frontispiece) suspended 2 m above the ground from a fork on a small branch in a black mangrove (*Avicennia marina*), 4 m in height.

Nash located the nest when one of the birds (probably the female) landed on it. While sitting on the nest, the female gave agitation calls and the nearby male began to sing. Within a few moments the female flew off the nest, and the male flew into it. The male sang while on the nest. At one point during these observations, a Bananaquit (*Coereba flaveola*) flew close to the nest and was promptly chased away by the male vireo.

The nest contained two eggs, glossy-white in color with small brown

spots on the wide end, and with finer brownish specks sparsely distributed over the remaining surface. The two eggs measured 19×12.5 mm and 18×13 mm.

The nest comprised a cup decorated on the exterior with shredded, brownish-leaf mulch, occasional bits of pale greenish and feathery, moldlike moss, and had a lining of fine grasses. There were several dead leaves hanging from the bottom of the nest. The dimensions of the nest were: inside diameter 40×50 mm, outside diameter 50×60 mm, inside depth 45 mm, and external depth 60 mm. The habitat at this site was swampy, with large clumps of scrubby mangrove growth, interspersed with areas where many shoots of mangrove were emerging from the wet, muddy substrate.

Nash found a second nest, which contained two unfeathered young about 2 days old, on 4 June 1983, as he walked several dozen meters south of the first nest along a path through pasture in which grew scattered breadfruit (*Artocarpus altilis*) and mango trees. A silent *V. caribaeus* flushed but stayed nearby. Immediately Nash discovered the nest 1 m up suspended from a small terminal fork in a broad-leaved shrub (species identity unknown) 1.3 m in height. This second nest was a deep cup measuring: outside diameter 50×60 mm, inside diameter 35×40 mm, inside depth 40 mm, and external depth 70 mm. As with the first nest, leaves and other plant matter held together by moss fibers formed the exterior, and fine grasses lined the interior. Dead leaves also hung from the bottom of the cup. The dimensions of both nests resemble those of nests of *V. b. bellii* (Barlow 1962).

At site #2 the nest shrub was shaded by a large breadfruit tree. Cattle grazed in the pasture but rarely came near the nest-site. The soil was dry in contrast to the swampiness of the first nest-site.

The female at nest #2 gave a slightly agitated, buzzing call while the male sang in 3-note couplets. Otherwise the birds seemed relatively undisturbed by Nash's presence.

At nest #2 the young showed increasing motor control and activity on 5 and 6 June and were visibly more reactive to noise than on 4 June. On 5 June both nestlings gaped when the adults approached. On 5 June Nash watched feeding of nestlings for 30 min, but saw only two trips made to the nest by the adults. Both sexes brought arthropods to the nestlings. By 6 June feather tracts were darkened on the nestlings in nest #2, and primaries and secondaries of these young were beginning to emerge. On 8 June the young showed fast-developing pterylae, and their eyes were beginning to open.

On 7 June at noon, nest #1 contained two naked nestlings, with eyes closed. The female flushed from the nest and gave the buzzing call when

Nash approached. The young were smaller than those in nest #2 at the time of the discovery of that nest on 4 June. No eggshells were in evidence at nest #1, but Nash surmised that the young had hatched in the early morning of the 7th as the nest had contained two eggs on the 6th.

At the two nests both sexes sat on the eggs, brooded, and fed the young. This is the pattern of parental sharing typical of species of the subgenus *Vireo* (Barlow 1962), which contrasts in part with species of the Red-eyed Vireo (*V. olivaceus*—subgenus *Vireosylva*) species complex in which males do not sit on the eggs during the incubation period (Barlow and Rice 1977, Barlow 1985).

Systematic relationships to other subgenus Vireo species. — When species of Vireonidae are grouped according to patterns of behavior, the results parallel intrafamilial classifications based on standard morphometric and phenotypic characters (Barlow and James 1975; Barlow 1980, 1981) and phylogenetic relationships indicated by DNA-DNA hybridization studies (Sibley and Ahlquist 1982). No behavioral traits, useful in assessing systematic relationships among vireos, demonstrated by *V. caribaeus* were found to differ substantially in this species from traits already described in other scrub-dwelling species (Barlow 1962, Barlow and Rice 1977).

Of primary importance from a behavioral perspective in assessing systematic relationships of *V. caribaeus* to other vireos is the fact that the nest is typically pensile and closely resembles in construction all other known vireonid nests—a factor regarded as diagnostic of the Vireonidae by Barlow and James (1975). Likewise the eggs are quite similar in size, color, and pattern to those of other vireos. What is known of adult behavior during incubation reveals participation by both sexes in diurnal incubation duties and brooding of the young, traits shared by all vireos except those of the *V. olivaceus* superspecies group (Barlow 1985). The structure and type of vocalizations, and the foraging behavior, clearly ally *V. caribaeus* with other scrub-dwelling species. Taken in concert, the traits enumerated above indicate the close relationship of *V. caribaeus* to other West Indian and continental "white-eyed" vireos.

SUMMARY

The St. Andrew Vireo (*Vireo caribaeus*) endemic to San Andrés Island, Colombia, was studied in April 1972 and June 1983. Territories were as small as 0.5 ha in area and were located in mangrove swamp and open-scrub and pastureland habitats. Gleaning of arthropods from leaves and twigs was the predominant foraging tactic used by *V. caribaeus*. Most foraging was no higher than 5 m in broad-leaved trees and shrubs.

Song consisted of three basic types (one, two, and three or more syllable types per song) which closely resembled those of other "white-eyed" vireos. Only three kinds of call notes were heard: single contact notes, *chee-chee* agitation calls, and a high-intensity "buzz" associated with nest defense.

The nest of the St. Andrew Vireo, described for the first time, is of standard vireonid construction. The two eggs of the first described clutch were a glossy-white with brownish spots ringing the wide end, typical of scrub-dwelling vireos. A second nest contained the first observed nestlings, which closely resembled those of other vireos. Both sexes sat on the eggs during the day, and both adults brooded and fed the nestlings. Collectively behavioral traits of *V. caribaeus* suggest that it is closely allied to other species in the subgenus *Vireo* occurring in the West Indies.

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COLOR PLATE

The Frontispiece of a St. Andrew Vireo (*Vireo caribaeus*) at a nest has been made possible by an endowment established by George Miksch Sutton (1896–1982). The painting is by J. P. O'Neill.