



WRENTHRUSH, *Zeledonia coronata*
From an acrylic-vinyl painting by John P. O'Neill
(three-fourths natural size)

A FIELD STUDY OF THE WRENTHRUSH,
ZELEDONIA CORONATA

JAMES H. HUNT

IN describing the monotypic genus *Zeledonia* Robert Ridgway (1888) wrote, "This remarkable new genus is so peculiar in its characters that I am in much doubt as to which family it belongs." For over 80 years systematists have shared Ridgway's uncertainty. Pycraft (1905), who published the only analysis of the Wrenthrush's anatomy, asserted, "there can be no doubt about the Turdine affinities of *Zeledonia*." He also established that *Zeledonia* has only 9 obvious primaries and 10 rectrices. These conflicting statements prompted Ridgway (1907: 885) to erect the monotypic family Zeledoniidae.

Since that time *Zeledonia* has been grouped either with the Turdidae (Mayr and Amadon, 1951; Ripley, 1952, 1964; Beecher, 1953) or in the family Zeledoniidae (Hellmayr, 1934; Eisenmann, 1955; Wetmore, 1960). Sibley (1968) presented new evidence from egg-white protein analysis showing that placement of *Zeledonia* in or near the Turdidae is incorrect. His findings indicate that *Zeledonia* is a true nine-primaried oscine, and Sibley (1970) has placed the genus in a monotypic tribe Zeledoniini, beside the tribe Parulini, in his family Fringillidae. The present paper presents evidence from a life history study that supports placement of *Zeledonia* among the nine-primaried oscines.

The Wrenthrush is found only in Costa Rica and western Panama. Slud (1964) cites records from the Cordillera de Tilarán, the Cordillera Central, the mountains bordering the southern edge of the central plateau, and the Cordillera de Talamanca. Hellmayr (1934) notes specimens from Volcán de Chiriquí in western Panama. Slud (1964) describes the distribution in Costa Rica as follows: "Vertically it ranges in the cloud-forested highlands from a low of about 4000 feet in some places, 5000-6000 feet in others, to timber line. It is quite common, particularly in the portions that are almost constantly drenched."

The morphological characters of *Zeledonia*, particularly the rounded

wings, abbreviated tail, and elongate tarsi, suggest that the bird is adapted for foraging in dense habitats. Carriker (1910), Slud (1964), and Morse (1966) are the only published sources on the behavior of the Wrenthrush, and each stresses its secretive habits.

While studying the Wrenthrush in its natural habitat I stayed at the restaurant-inn La Georgina in Villa Mills, Costa Rica, on the Carretera Interamericana between Cartago and San Isidro del General. La Georgina is at an elevation of 3,100 m, approximately 5 km east of Cerro de la Muerte, now shown on some maps as Cerro Buenavista. I made field studies of Wrenthrushes on 101 days during the period 17 February to 3 July 1968, taking notes on the species' behavior and ecology. I caught three Wrenthrushes with mist nets and marked them with colored aluminum leg bands for individual recognition.

THE STUDY TRACT AND ITS VEGETATION

The study tract (Figure 1), a small ravine 0.75 km southeast of the restaurant-inn La Georgina, is one of the many sharply contoured small valleys in the vicinity. Approximately 1.8 hectares in extent, the elevation at its floor is approximately 3,050 m. It shows a relief of at least 25 m from its crest to its floor and is more than 100 m wide at its widest point. The east and west sides are the natural hillsides, while the southern closure is the steep roadbank of the Carretera Interamericana. The northern limit is marked by a waterfall over which a small stream cascades some 10 m into a confluent ravine below.

Vegetation of the ravine was typical for the region. *Quercus costaricensis* was the dominant tree. Other large trees included *Didymopanax pittieri*, *Drimys winteri*, *Weinmania pinnata*, and *Oreopanax nubigena*. Shrubs in the understory included *Solanum storkii*, *Clethra gelida*, and *Miconia* spp. Dense tangles of *Rubus* sp., *Centropogon* spp., *Veronia* (?) sp., and other herbs covered large areas in the understory. A bamboo, *Chusquea serrulata*, grew in single-species stands as the major understory plant in some parts of the ravine. Epiphytes of many kinds covered most available portions of the larger trees and shrubs. Ferns and mosses were extremely abundant both as epiphytes and on the ground, and a few treeferns (*Alsophila* sp.) were present.

Herb, shrub, and tree layers were well-marked over most of the tract, but the shrub layer sometimes merged with the herb layer and was sometimes absent. Peripheral portions of the tract, where *Chusquea* dominated the understory, displayed only two layers, the *Chusquea* and the canopy.

The herb layer, which was of particular importance in this study, varied considerably within the tract. It ranged in height from less than 0.3 to more than 2 m, exclusive of the mature *Chusquea*, which was often

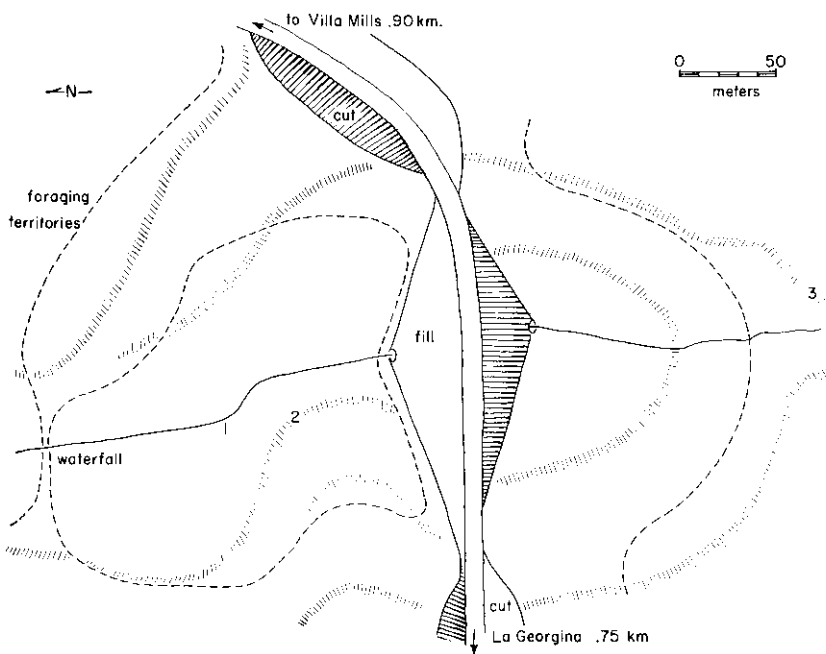


Figure 1. Sketch map of the study tract and vicinity. The Inter-American Highway is shown cutting across a ravine, with the study tract north of the road fill. A small creek flows beneath the highway and north through the tract. The dotted lines indicate approximate foraging boundaries for three pairs of Wrenthrushes, and the numbers indicate the approximate locations of the three nests found.

3 m or more high. The dense tangles of vinelike herbs, ferns, and low shrubs were common, and often had a distinct surface layer of foliage and a dark, leafless interior. The stands of mature *Chusquea* resembled these tangles in having an outer surface of foliage and an open and leafless interior. The *Chusquea* foliage was often more than a meter deep with an open stratum of 2 m or more beneath. In other areas the herb vegetation was more open and more uniformly foliated.

As rain and fog occurred almost daily during my study, the vegetation was frequently wet. The moss in particular and the surface of the ground were almost always soaked and wet to the touch.

VOCALIZATIONS

Vocalizations of the Wrenthrush are distinct and are easily identified when one is familiar with them. They play an apparently major role in the species' behavior, and listening for them was the easiest way to find the bird in the field. The vocalization most often heard is what I henceforth

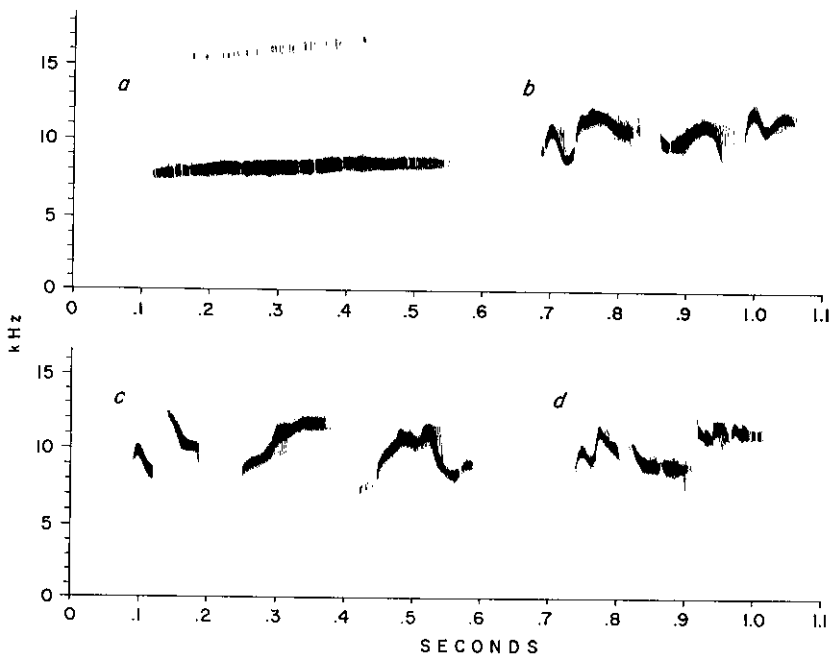


Figure 2. Tracings of sonagrams of the call (a) and three song figures (b, c, d) of *Zeledonia coronata*. The sonagrams were made at one-half the original recording speed.

refer to as the call. It has been variously described as "a clear, musical whistle" (Carriker, 1910: 332), as "a rather long, level, penetrating thin whistle, something like 'seenk'" (Slud, 1964), and as "somewhat suggestive of low-volume calls of the Swainson's Thrush (*Hylocichla ustulata*) or of the spring peeper (*Hyla crucifer*), although sounding slightly more like a whine" (Morse, 1966). The call (Figure 2) sounds to me like a thin, penetrating, high-pitched whistle, usually with a slight rising inflection, best phoneticized as "sseeeee." A typical call lasts about 0.5 second.

The other major vocalization, heretofore undescribed in the literature, I shall refer to as the song (Figure 2). It is similar to the call in being high-pitched and rather thin in tone quality. The complete rendition is a sequence of variable figures spaced at regular intervals and forming long phrases. Typical figures can be phoneticized as "ssee-del-deet" and "ssee-del-döt," with emphasis on the last syllables. The figures are squeaky and would not be considered musical by most listeners. Pauses between figures were noted in the field to range from 0.5 to as much as 5 seconds.

The Wrenthrushes on the study tract called or sang throughout the day. They typically called only once or twice and then were silent for periods of a few minutes to several hours. Occasionally a bird gave a series of calls spaced at intervals of a few seconds and continuing for several minutes. Songs were heard less frequently than calls, but a series of song figures usually lasted several minutes. Series lasting 2 to 5 minutes were typical, and series lasting 10 minutes were not uncommon. The longest series I heard was from a single bird that sang a figure every 3 to 5 seconds for just over 27 minutes.

I heard several other Wrenthrush vocalizations, but none were as common as the call and song. I provoked a male I had netted into uttering a number of distress calls. These were rather harsh, rasping sounds that I never heard on another occasion. A female once gave a dry, toneless "chip" while carrying nesting material in her bill headfirst down a moss-covered tree trunk. Except for this single note I did not hear the chip notes mentioned by Morse (1966). Nestlings less than 5 days old gave thin, high "peep" calls like those of most small birds. Calls of older nestlings were toneless and sounded like a combined hiss and buzz.

GENERAL OBSERVATIONS

Zeledonia coronata was difficult to watch in the field. The extremely dense habitat that the birds frequented made collecting data systematically almost impossible. Thus the following statements on Wrenthrush behavior are the synthesis of isolated observations.

I regularly encountered solitary Wrenthrushes and occasionally saw or heard two of the birds together. Only two individuals, one male and one female, were present on the study tract. The adjoining ravine, approximately 1 hectare in extent, and the ravine across the road from the tract each had only one pair of the birds. During my study I neither saw nor heard more than two adult Wrenthrushes in any ravine.

The rugged topography near Villa Mills seems to favor this pattern. Ridgetops apparently serve as rather distinct boundaries. The Carretera Interamericana, which transversely bisects many ravines and ridges north of the main mountain ridge, is also an effective boundary. The Wrenthrushes on the study tract foraged throughout the ravine, though they apparently did not forage on the ridgetops, on the roadbank, or into the adjoining ravine. The physiographic boundaries alone seemed to determine foraging limits on three sides of the tract, but behavioral interaction with the pair in the adjoining ravine may have determined the northern limit.

Several times when one or both birds on the tract were calling or singing I heard one or both Wrenthrushes in the adjoining ravine begin to sing. Sometimes when this happened I could move quickly to near the

small waterfall and see one or both birds in the ravine below hopping about as they sang. Though the birds in the adjoining ravine often sang beside the waterfall, the two on the study tract never came closer to it than 10 m. Occasionally all four sang simultaneously, but none showed any obvious excitement; they appeared simply to be foraging as they sang. Singing by the birds on one tract was apparently in direct response to singing by birds on the other. Though I never saw territorial display I believe the countersinging served to maintain the boundary.

The sexes of *Zeledonia coronata* are identical in plumage and sing with equal proficiency. Only behavior associated with vocalizations provided a clue to sex identification. When one bird called while foraging alone the other sometimes answered in call or song. If the first bird repeated its call, the other often hopped or flew to join it. Color-banding and subsequent collecting showed the bird that moved to join its mate was the male.

The Wrenthrushes I watched foraged only in the herb layer of the forest. On the few occasions when I saw one above that stratum, it was in tangles of vines and epiphytes on the trunks and lower limbs of trees. These tangles had the same apparent denseness as the herb layer and seemed to be, in effect, only vertical extensions of the herb habitat. The birds concentrated their activities in particular portions of the herb layer by consistently selecting concealed rather than exposed foraging sites. They foraged well inside vegetation tangles with foliated exteriors and leafless interiors, while in more uniform vegetation they selected foraging sites that seemed to be as concealed as possible. In stands of mature *Chusquea* they foraged on or near the ground, but not in the foliage or near the periphery of the stand. Even in places where the herb layer was 0.3 m or less in height, the birds foraged on or near the ground rather than in exposed portions of the vegetation. I measured 25 perches on which I saw the birds; they ranged from 4 to 30 mm (mean = 13 mm) in diameter and 0° to 85° (mean = 30°) in inclination.

Wrenthrushes hop when moving on the ground and from perch to perch. I rarely saw a Wrenthrush use its wings during its hops, but wing-flicking was common. A bird perching or standing between hops sometimes extended and retracted its wings with a rapid flicking motion. The wings were never more than half-spread in these flicks. After one or two quick wing flicks the bird usually hopped to another perch, perhaps wing-flicked again, and then moved on, wing-flicking occasionally as it foraged. This behavior served no obvious display or feeding function. I saw male and female birds flick their wings both when foraging alone and with the other member of the pair.

The Wrenthrush is apparently an extremely weak flier. The birds I

watched rarely flew, but when they did they exhibited a characteristic flight pattern. A bird always launched off a perch from which it could glide or flutter downhill. Wing beats were extremely rapid and apparently incapable of sustaining long flights. The Wrenthrushes could steer around objects and control their direction and rate of descent, but I never saw one abruptly change direction or fly directly from a low perch to a higher one as do passerines of average flying ability. Most flights I saw covered less than 10 m, but a bird sometimes flew 20 m or more from high on the side of a valley.

The typical sighting of a Wrenthrush was a brief glimpse as the bird hopped out of, then immediately back into, the dense vegetation. The brief look was usually enough to note only the general direction a bird was moving and to identify it if it was banded. I found that by noting carefully the direction a Wrenthrush was traveling I could sometimes move around or ahead of it along one of several cowpaths crossing the tract and intercept it as it crossed the path. By again noting the bird's direction and moving to another position on another cowpath, I could perhaps see it once more as it continued on its way. This was the only method by which I could follow the birds.

On 17 April the strategy just described allowed me to record my longest continuous series of observations. I located the foraging pair high on one edge of the tract. From this point they moved slowly together in a large loop down through the center of the ravine, and I finally lost them near where I first found them. The total linear distance covered was slightly more than 200 m, and the time from the first to the last sighting of the pair was 1 hour and 55 minutes.

Twice I saw a Wrenthrush preening. Both times the bird was well-concealed in the dense, tangled vegetation, and I could note only that the bird scratched its head directly, that is, under the wing.

Once I saw a Wrenthrush react to the presence of a bird of another species. The pair of Wrenthrushes I was following was hidden from view inside a dense thicket. A mixed flock of birds moving above that thicket included several Sooty-capped Bush-Tanagers (*Chlorospingus pileatus*). One of the bush-tanagers was perched on an exposed branch about 0.3 m above the thicket when the male Wrenthrush suddenly sprang from the thicket toward the bush-tanager, causing it to leave, and landed where it had been. A sharp "chip" was sounded the instant the supplanting occurred, but I could not tell which bird made the sound. The supplanted bush-tanager flew to a branch about 2 m away. The Wrenthrush turned, pecked once or twice at the perch, and then dropped back into the thicket and out of sight.

Wrenthrushes responded variously to my presence. If I happened to

come suddenly upon a foraging bird, it acted startled, called once loudly, and hopped quickly away. If I heard an unseen Wrenthrush calling and made noise penetrating the vegetation toward it, it hopped away; but if I sat or stood quietly, a foraging bird sometimes passed near me, apparently ignoring my presence. Thus the birds seemed to respond to movements and to sounds that I made, but not to my presence if I was motionless and silent. The only consistent exception was the birds' reaction to my presence near an active nest even when I stayed still.

The three Wrenthrushes I captured in mist nets behaved in the hand much like other small songbirds. After a few attempts to fly away, each sat quietly while I held it. As I color-banded the birds, each ineffectually bit my fingers. Only the bird that gave the distress call described earlier made any sound. I released the birds by tossing them up to see if they would fly away. None did so. Each fluttered to the ground, darted quickly into the nearest vegetation, called once or twice, and then disappeared.

NEST, EGGS, AND YOUNG

A Wrenthrush singing on 19 March was the first sign of possible breeding activity to attract my attention. The song was distinctive, and I noted it as being unusual before I identified the singer. I may have heard the song before this date and let it pass unnoticed, but its striking qualities cause me to doubt this. It was stilted in rhythm and phrasing, but 3 or 4 days later it changed noticeably to the smoother phrasing described earlier. By 22 March the male and female were both in song and were foraging together frequently. Previously I had rarely seen the birds together, and I had not been sure that only two Wrenthrushes were on the tract.

At 10:30 on 25 March I was sitting on the bank of the small stream in the lower central portion of the ravine. The two Wrenthrushes had been singing just out of sight downstream, and they soon came hopping through the dense vegetation only 3 or 4 m to my left. One was carrying a small tuft of moss in its bill. That bird hopped to a spot less than 0.5 m from my feet and just out of sight over the crest of the creek bank. After rustling the vegetation for a few seconds the bird rejoined its mate, no longer carrying the moss. The pair moved quickly downstream, reappeared a few minutes later, and repeated the performance. Both birds brought moss several times during the next few minutes, but by 11:00 they had left the area. I then examined the moss-covered bank and found the nest.

The gully through which the shallow creek flowed was about 2 m wide at the nest site, and its banks were about 1.25 m high. The nest filled a cavity in a heavy growth of moss covering a vertical, flat-faced portion of the west bank. The front of the nest was flush with the outer face of the moss and was thus extremely inconspicuous. The cavity was situated

near the crest of the bank just below where the gentle slope of the valley floor dropped abruptly into the gully. Dense herb and shrub growth arching low over the gully completely concealed the nest site.

The nest was a domed structure built entirely of mosses with its opening facing the creek. It was incomplete when I found it, so I selected a spot about 5 m upstream where I could watch the site yet remain out of the birds' zone of activity. As I could not see the nest itself from my vantage point, I am unable to describe the construction process, but I examined the nest and wrote a description of it each afternoon of the construction period:

25 March: a spherical structure about the size of a softball; domed roof complete; thickness of wall about 2 cm and uniform throughout; opening in side about 8 cm in diameter; floor of nest about 2 cm below bottom rim of opening.

26 March: diameter of opening reduced to about 5 cm; much material added to the bottom rim giving it a thick, rounded appearance; depth of cavity below rim of opening now about 4.5 cm.

27 March: opening now an oval about 4.5 cm wide by 3.5 cm high; much material added to the upper rim of the opening giving it the thick, rounded appearance of the bottom rim.

28 March: appearance much as on 27 March; some material added to roof and some to the outside below the opening to form an "apron."

29 March: as on 28 March, but with some material added within the cavity making it a bit more shallow, more rounded in the bottom, and softer to the touch.

30 March: exterior unchanged; floor of cavity not so soft, but smoother and more shallowly rounded; for the first time feels like a formed, well-shaped nest cup.

31 March: exterior unchanged; nest cup with a shallow lining of dead, dry plant material.

The nest was essentially complete on 31 March. I watched construction for 7 days and guess that the nest was in at least the second day of construction on 25 March. My notes describe the completed nest (Figures 3 and 4) as follows:

A domed nest with an entrance in the side; maximum outside height 20 cm; maximum outside dimension, side to side, 16 cm; maximum outside dimension, front to back, 10 cm; opening 4.5 cm wide by 3.5 cm high; nest cup 7 cm side to side, 5 cm front to back; inside height, floor to roof, 9 cm; floor of nest cup 2.5 cm below rim of opening; roof 4 cm thick; right wall 5 cm thick; left wall 3 cm thick; bottom 7 cm thick; construction material mostly mosses plus a few small leaves and limber twigs, all tightly pressed together; nest cup lined with fine dead plant material, including small fragments of grasses, thin shafts of dead and decayed leaves and mosses, and fragments of fragile skeletons of decaying leaves.

As Table 1 shows, the female did most of the work in the early stages and then completed the nest alone. Nest-building activity was concentrated in the mornings. Both birds were working on the nest when I left at 11:30 on 25 March, but neither appeared between 13:00 and 16:00 that after-



Figure 3. The first nest. Vegetation overhanging the site has been removed; the arrow indicates the nest opening.

noon. On succeeding days work was in progress when I arrived at the site, usually at about 07:30, and on these days the last recorded visit to the nest was as follows: 10:45, 10:56, 11:28, 09:10, 09:55, and 09:43. Observations during the afternoons showed no visits by either bird.

During the week following construction I noted the pair foraging together and singing frequently, but I neither saw nor heard them near the nest during this period. I feared the nest had been abandoned, but on the morning of 8 April I found one egg therein. The egg was unattended, and I did not see the birds near the nest that day. Late in the afternoon I collected the egg, prepared it as a museum specimen, and saved its



Figure 4. The first nest after removal from the bank.

albumin for electrophoretic analysis. A second egg was laid on 10 April. Though I left the second egg untouched, I never again saw a Wrenthrush near the nest.

Eventually I collected the second egg and prepared it, too, as a museum specimen. The eggs (Figure 5) are short subelliptical in shape but are otherwise somewhat dissimilar. The first was a little larger, being 2.19 by 1.73 cm, while the second was 2.12 by 1.69 cm. The first was white with irregular light brown spots. The second was white or buffy white with its brown spots smaller, more numerous, and more evenly distributed.

The pair continued to forage together and sing frequently after abandoning the nest. I watched them closely for more than a week but saw no

TABLE 1
TRIPS TO NEST WITH NESTING MATERIALS BETWEEN 08:00 AND 09:00

	26 March	27 March	28 March	29 March	30 March	31 March
Male	25	23	0	0	0	0
Female	59	33	18	20	19	11

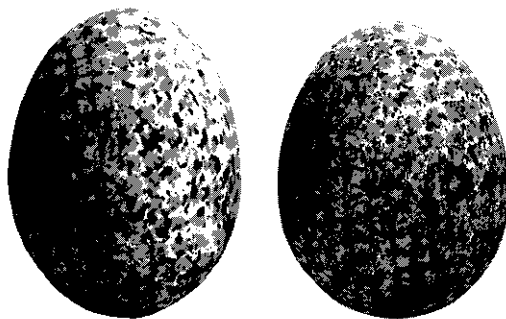


Figure 5. Eggs ($\times 2$) of *Zeledonia coronata*. The albumin sample was taken from the first-laid egg at left.

indications of attempted renesting. Therefore I let observations on the study tract lapse while watching Wrenthrushes elsewhere. I found no sign of nesting activity in those areas, and on 28 April I returned to the study tract. On that morning I located a singing pair and noticed it did not include the original color-banded male. The original female had not been banded, so I could not tell whether only the male or both birds were new. As they were definitely foraging as a pair, I netted and color-banded them both and resumed watching on the study tract.

The birds' activities seemed to be mostly foraging plus occasional singing. I noticed no unusual behavior nor signs of nesting activity until 19 May when I saw the female carrying a billful of insects. That indicated she was feeding young, and I began watching her as closely as possible. I finally found the nest the morning of 21 May.

The second nest was identical to the first in appearance and construction, and it also was concealed in a vertical, moss-covered bank. The bank was on the steep west slope of the valley at least 15 m above the creek. Vegetation at this point was a *Quercus* overstory with a dense *Chusquea* understory approximately 4 m high and leafless in the lowest 2 m. The ground was covered with leaf litter, and heavy growths of moss covered exposed roots and logs and places where litter did not accumulate such as the vertical bank. The bank containing the nest was 0.5 m wide by 0.5 m high and was, in reality, only a sharp irregularity in the steep slope of the hill.

The nest contained two young Wrenthrushes. They were altricial and pilopaedic and appeared to be not more than 3 days old. The eyes were still closed. The bills were yellow externally, not well-developed, and lacked any egg tooth. The color of the mouth lining was an orange hue similar to the color of the mouth and of the crown patch in adults. The

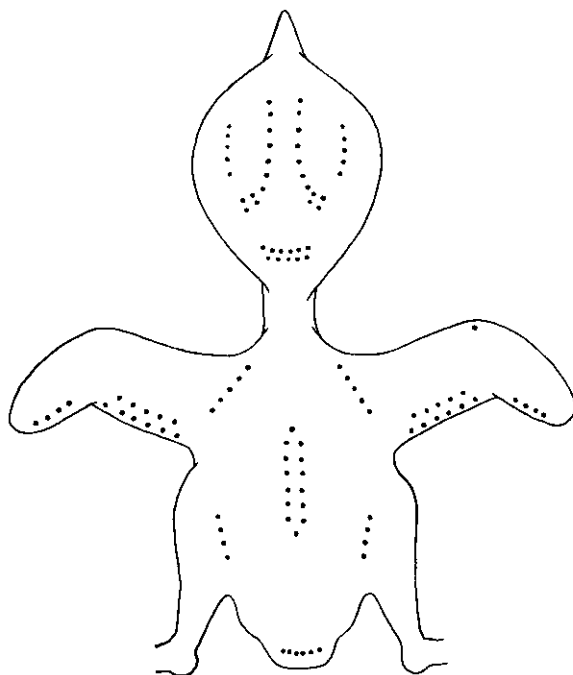


Figure 6. Distribution of neossoptile tracts in a juvenal *Z. coronata*. The specimen, LSUMZ 64818, was collected 22 May 1968 when approximately 4 days old. The method of illustration is after Wetherbee (1957); no attempt is made to show individual feathers.

birds sat side by side in the nest cup facing the opening. When I tapped the nest they gaped toward the opening and gave the peeping sound mentioned earlier. When not gaping and peeping, they rested with their chins on the rim of the nest cup, still facing the opening.

The nature of the site made a blind impractical, so I chose a spot 5 m away near a fallen log where I could remain semiconcealed but still watch the nest. The adults seemed to notice me, however, no matter how still I kept. The female sometimes passed near me, but still she seemed wary. Twice the male (not carrying food) followed the female to the nest, and both times he noticed me and hopped quickly away. As a result I limited observations to 3 hours per day.

Only the female fed the young. She brought insects, including lepidopteran larvae, but I was unable to identify most food items. She brooded the young after most of the feedings. The average of 18 periods of brooding was 14.3 minutes (range 9 to 19). After brooding she flew downhill 8 m or more directly from the nest and then called once or twice.

TABLE 2
LENGTH AND COUNTS OF NEOSSOPTILES OF *ZELEDONIA CORONATA*¹

Region	Length	Left	Right
Coronal	15	16	15
Orbital	6	9	10
Occipital	17		15
Scapular	12	5	5
Lesser secondary covert	9	6	6
Greater secondary covert	13	10	10
Greater primary covert	2	5	5
Alular	1	0	1
Dorsal	17		18
Caudal	1		11 ²
Femoral	12	5	4

¹ One specimen (LSUMZ 64818), approximately 4 days old. Method of analysis and presentation after Wetherbee (1957).

² Five left of midline and six right of midline; none distinguishably different from the others.

The male usually responded in song from somewhere outside the *Chusquea* thicket, and I sometimes heard the pair singing as they foraged together before the female returned. The average of 16 periods of absence of the female from the nest was 20.3 minutes (range 5 to 36).

One nestling was dead on 22 May, the day after I found the nest. During 12 hours of observation on 22 through 25 May the female fed the remaining nestling only 22 times, an average of 1.8 feedings per hour. On 26 May the second nestling was dead. The effect of my presence may have caused the nest failure, but whatever the primary cause, the nestlings apparently starved to death. I preserved the first nestling in formalin and prepared the second as a study skin. Figure 6 and Table 2 show the neossoptile distribution on the younger specimen. On 27 May I collected the adult birds and confirmed my identification of their sexes.

I found a third nest on 26 June in the ravine across the highway from the original study tract. It was similar in construction to the first two and was placed in the center of a vertical, moss-covered bank 1.25 m high by 1.50 m wide. A dense shrub canopy concealed the site, but the nest itself was below this canopy and the space around it was open and leafless. The nest contained two nestlings whose plumage, as compared to that of the previous ones, showed them to be about 10 days old. Again the surroundings were unsuitable for a blind, so I made only daily spot checks on the nestlings and left the nest otherwise undisturbed. By 1 July the birds were fully feathered, and I collected one for museum preservation. On 3 July, the last day of my study in Villa Mills, I collected the remaining nestling and an adult that was bringing it food. The adult was a male, suggesting that in this successful nesting both parents fed the young.

The juvenals of *Zeledonia coronata* are pictured in Figure 7. The

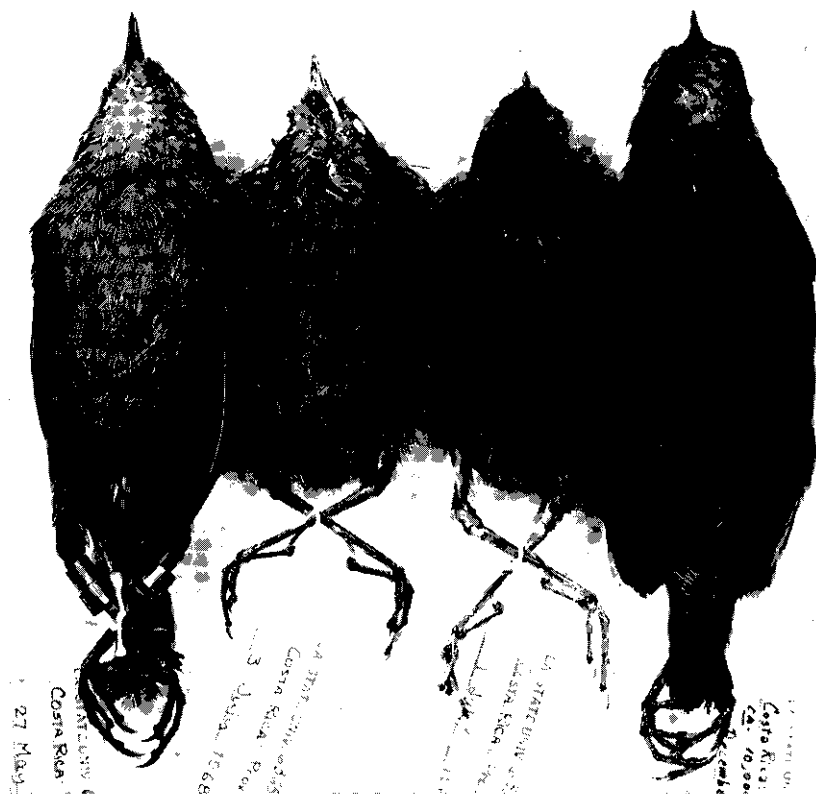


Figure 7. *Zeledonia coronata* nestlings between two adult males (females are similar). The young birds are approximately 17 (left) and 15 (right) days old.

plumage is similar in color and pattern to that of the adults. The oldest nestling shows faint traces of orange on its crown. The young birds have no spotting.

DISCUSSION

Egg-white protein analysis by Sibley (1968) clearly demonstrated that the relationships of *Zeledonia coronata* are with the New World nine-primaried oscine assemblage. His study included a review of previously confusing characters of the Wrenthrush's morphology and a comparison of these characters with those of typical nine-primaried forms. In concluding his study Sibley (1968: 9) wrote: "It is not possible, from the egg-white data alone, to determine to which of the several groups of 'nine-primaried' oscines *Zeledonia* should be assigned. In its morphology, however, it seems closest to the wood warblers." The larger work by Sibley (1970) on

passerine egg-white proteins placed all nine-primaried oscines (except Vireonidae, Vireolaniidae, and Cyclarhidae) in a single family, Fringillidae. Within this group *Zeledonia* is placed in a monotypic tribe beside the wood warblers. Sibley (1970: 107) says: "I have placed it adjacent to the Parulini but in a separate tribe, Zeledoniini, in recognition of its specialized characters and to call attention to its new location in the classification." In the present paper I will not discuss this or other possible taxonomic placements of *Zeledonia*. Field study data on the Wrenthrush cannot answer the question of its systematic relationship. As the life history data are of taxonomic value, however, a review of comparative data from among the wood warblers may aid in future systematic studies.

The Wrenthrush's nest is a domed structure made mainly of moss and placed within a cavity in a bank with the nest opening facing one side. Skutch (1954: 384) writes: "Usually the wood warbler's nest is a simple, cup-shaped structure, but in *Myioborus*, *Basileuterus*, *Ergaticus* and *Seiurus aurocapillus* it is a roofed, oven-shaped construction with a round doorway in the side, placed in a niche in a bank or cliff, on a steep slope, or, in the last-mentioned species, on level ground." None of the nests Skutch describes (1954, 1967) were made of moss as were the Wrenthrush nests I found, but Dickey and van Rossem (1938: 506) tell of a nest of *Myioborus miniatus* made of moss and remarkably similar in description to the Wrenthrush's.

Eggs of the Wrenthrush are white with light brown spots. Skutch (1954: 384) writes: "The eggs of wood warblers are usually white or cream or are lightly tinted with green, blue or pink, rarely with deeper green, and in nearly all species they are more or less heavily spotted or blotched with shades of brown, chestnut, lilac or black, the markings as a rule heaviest on the large end, where they form a cap or wreath." Thus Wrenthrush eggs fall within the range of variation Skutch describes for parulids, but the almost uniform spotting of the Wrenthrush eggs is somewhat different from the typical parulid pattern of a concentration of markings at the larger end. The short subelliptical shape of the Wrenthrush eggs shows little tapering toward the small end, whereas many wood warblers tend toward oval or short oval shape, with a somewhat pointed small end. The size of the Wrenthrush eggs is also noteworthy. In fact, G. H. Lowery, Jr. (pers. comm.) points out: "the eggs of no warbler that I have examined, except those of some *Icteria virens*, appear larger. To express the matter somewhat differently, the eggs of *Zeledonia* seem larger in relation to the body size of the bird than those of any parulid."

The three known nests of the Wrenthrush each had a clutch size of two. Skutch (1954) says that *Basileuterus fulvicauda* commonly has a clutch of two eggs, and species of *Myioborus* and *Ergaticus* are known to lay as few

as two. These seem unusual, for he writes (Skutch, 1954: 384) that "even within the tropics the sets of most species of warblers average larger."

Incubation period and incubation behavior in the Wrenthrush remain unknown. Nestling period in the species is long, with one specimen collected from the nest at an estimated 17 days of age. Skutch (1954: 385) notes that periods for North American warblers range from 8 to 10 (rarely 11) days, while those of two Central American species of *Myioborus* range from 12 to 14 days and *Basileuterus fulvicauda* ranges from 12 to 15 days. The Wrenthrush, if my estimate is correct, has a longer nestling period than typical warblers.

Mouth color of the nestling Wrenthrushes found 21 May was noted to be the color of a Kodak film package anteriorly and deeper orange (the color of the crown patch in adults) toward the rear. In her review of passerine nestling mouth color as a taxonomic character Ficken (1965) notes that the lining color is usually a good family character, but some groups, including the parulids, show intrafamilial variation. Typical parulids have red mouth linings, but those of species of *Basileuterus* and *Myioborus* were yellow, and of *Cardellina rubrifrons* and *Setophaga picta* orange-yellow. The Wrenthrush, using Ficken's terminology, would probably be described as orange-yellow or yellow, not red. In discussing the species mentioned Ficken (1965: 74) writes: "These warblers are the only nine-primaried oscines for which information is available which have yellow mouth linings. This probably indicates that *Myioborus*, *Basileuterus*, *Cardellina rubrifrons*, and *Setophaga picta* are a closely related assemblage. They are probably not very closely related to the wood warblers and their morphological resemblances may be the result of adaptations to similar feeding habits."

The young of *Zeledonia* (in which adults show no sexual dimorphism) were found to develop a juvenal plumage that strongly resembles the adult plumage. The 17-day old nestling is very similar in overall coloration to adult birds and shows faint traces of orange on its crown. Regarding the plumage of immature parulids Skutch (1954: 385) comments: "The acquisition of the adult plumage is strikingly different in the migratory and non-migratory members of this family. Young males of the migratory species go south in the immature plumage, pass the winter in that plumage, and then take on the bright nuptial attire before returning to their breeding grounds in the north. In the non-migratory Central American species of *Myioborus*, *Basileuterus* and *Ergaticus*, the sexes of which are alike, the young of both sexes acquire a plumage essentially like that of the adult soon after leaving the nest." The pattern of development shown by *Zeledonia* coincides with the genera mentioned, but this pattern is not

characteristic of tropical parulids only, for Skutch (1957: 277) notes a contrast among migratory and nonmigratory icterids and tanagers similar to the one quoted for wood warblers.

Thus *Zeledonia coronata* seems similar in several life history characters to species of the tropical wood warbler genera *Myioborus*, *Basileuterus*, and *Ergaticus*. These similarities do not, however, coincide in exact detail, minor differences being noted in most comparisons. Furthermore it should be stressed that similar life history characters appear in passerine species unrelated to the parulids. Of what value, then, are these data, especially when one considers the evolutionary phenomenon of convergence in adaptive strategies?

Speciation of the Wrenthrush *in situ* in the Central American mountains seems probable. Sibley (1968) has suggested the bird resembles parulids morphologically. The species does not appear closely allied to any group other than parulids, and a common ancestry with tropical parulids is both possible and plausible. The similarities of life history characters between the Wrenthrush and tropical parulids thus enhance the plausibility of this theory. In no case do the life history data clearly demonstrate the Wrenthrush to be a warbler, but, more importantly, no life history detail precludes that relationship.

Unique morphological features of the Wrenthrush include its short rounded wing, abbreviated tail, and reduced carina. All are associated with the near flightlessness of the species and seem highly adaptive for its foraging mode and habitat selection. No species now recognized as a parulid shows such marked morphological modifications. Thus these features serve to distinguish the Wrenthrush from its suggested near relatives, even though these features may be largely adaptive in nature. Similar morphological features involving adaptation to similar life habits are found among species unrelated to parulids, notably the Rhinocryptidae.

At present the exact relationships of the Wrenthrush remain unknown. Morphological analysis by Sibley (1968) indicates possible relationship with parulids, and life history characters presented here show similarities with tropical warbler genera. Family delineation within the nine-primaried oscines is unsettled at best, and it has even been suggested (Sibley, 1970: 107) that the recognized groups often considered as families may represent major feeding niche groups, not genetically related entities. The possibility exists, however, that *Zeledonia coronata* shares phyletic relationship with a group including the several tropical warbler genera discussed.

ACKNOWLEDGMENTS

I wish to acknowledge with sincere thanks the contributions of the following persons. W. H. Buskirk, R. K. Colwell, M. M. Colwell, J. A. Feduccia, A. L.

Gardner, and W. H. Hatheway aided in the field. Charles G. Sibley generously shared his comments on *Zeledonia*. Personnel of the Organization for Tropical Studies in San Jose, Costa Rica provided field equipment and secured my collecting permits. Personnel of the International Center for Medical Research and Training in San Jose, Costa Rica, especially Dr. Victor Villarejos and Señor Fernando Granados, were particularly responsible for making my stay in Costa Rica as pleasant and profitable as it was. Gene M. Christman assisted in preparing several figures.

Support for this study was provided by a research assistantship from the Louisiana State University Museum of Zoology. Travel funds were provided by grants to the Louisiana State University Museum of Zoology by Edward McIlhenny Simmons and the Louisiana Research Foundation and by the Judith D. Ambrose Memorial Fund.

I am indebted to John P. O'Neill for his superb portrait of the Wrenthrush and to Mr. John S. McIlhenny of Baton Rouge, Louisiana for underwriting the costs of reproducing it as the frontispiece of this volume.

I thank Douglas A. Rossman, Harry J. Bennett, and Walter J. Harman who read a draft of this paper as part of a Master of Science thesis. Special thanks are due Robert J. Newman for his careful editorial review of several drafts of the paper. Most especially I wish to thank George H. Lowery, Jr. for his direction, support, and encouragement throughout the course of the study.

SUMMARY

Field studies of *Zeledonia coronata* verify the impressions of earlier observers that the species is very secretive. Wrenthrushes select foraging sites in concealed portions of dense herb and low shrub vegetation. The combination of secretive habits and dense habitat render the species nearly impossible to locate except by its characteristic vocalizations, particularly the call, which are easily heard within the habitat. Calls and song seem to serve as communication between members of a pair, and countersinging between neighboring pairs was noted. Wrenthrushes are distributed in the Villa Mills vicinity in widely separated pairs, though the rugged topography of the region may be a causal factor in this pattern. The birds hop along the ground or from perch to perch in foraging the dense vegetation, and they fly only rarely. The flight of Wrenthrushes is weak, and the birds usually fly less than 20 m before landing. Wrenthrushes pay little attention to birds of other species and, except when nesting, seem unconcerned of human observers who remain motionless and silent. Nests of *Z. coronata* are domed structures made mainly of moss and are concealed within vertical, moss-covered banks. The eggs are white or buffy white with light brown spots. The juvenal plumage resembles that of the adults.

The work of Sibley (1968) is cited as showing that *Z. coronata* is a nine-primaried oscine. Similarities in life history between *Z. coronata* and several tropical wood warblers are examined, and it is suggested that these several forms may represent a genetically related phyletic group.

LITERATURE CITED

- BEECHER, W. J. 1953. A phylogeny of the oscines. *Auk*, 70: 270-333.
- CARRIKER, M. A. 1910. An annotated list of the birds of Costa Rica including Cocos Island. *Ann. Carnegie Mus.*, 6: 314-915.
- DICKEY, D. R., AND A. J. VAN ROSSEM. 1938. The birds of El Salvador. *Field Mus. Nat. Hist., Zool. Ser.*, 23: 1-609.
- EISENMANN, E. 1955. The species of middle American birds. *Trans. Linnaean Soc. New York*, 7: 1-128.
- FICKEN, M. S. 1965. Mouth color of nestling passerines and its use in taxonomy. *Wilson Bull.*, 77: 71-75.
- HELLMAYR, C. E. 1934. Catalogue of birds of the Americas and the adjacent islands. *Field Mus. Nat. Hist., Zool. Ser.*, 13, part 7: 1-531.
- MAYR, E., AND D. AMADON. 1951. A classification of recent birds. *Amer. Mus. Novitates*, 1486: 1-42.
- MORSE, D. H. 1966. Notes on the Wren-thrush. *Condor*, 68: 520-521.
- PYCRAFT, W. P. 1905. On the systematic position of *Zeledonia coronata*, with some observations of the position of the Turdidae. *Ibis*, 5, 8th Ser.: 1-24.
- RIDGWAY, R. 1888. Notes on Costa Rican birds, with descriptions of seven new species and subspecies and one new genus. *Proc. U. S. Natl. Mus.*, 11: 537-546.
- RIDGWAY, R. 1907. The birds of North and Middle America. *U. S. Natl. Mus., Bull.* 50, part 2.
- RIPLEY, S. D. 1952. The thrushes. *Postilla*, 13: 1-48.
- RIPLEY, S. D. 1964. Subfamily Turdinae. Pp. 13-227 in *Check-list of birds of the world*, vol. 10 (E. Mayr and R. A. Paynter, Jr., Eds.). Cambridge, Massachusetts, *Mus. Comp. Zool.*
- SIBLEY, C. G. 1968. The relationships of the "Wren-Thrush," *Zeledonia coronata* Ridgway. *Postilla*, 125: 1-12.
- SIBLEY, C. G. 1970. A comparative study of the egg-white proteins of passerine birds. *Peabody Mus. Nat. Hist., Bull.* 32.
- SKUTCH, A. F. 1954. Life histories of Central American birds, families Fringillidae to Coerebidae. *Pacific Coast Avifauna*, No. 31.
- SKUTCH, A. F. 1957. The resident wood warblers of Central America. Pp. 275-285 in *The warblers of America* (L. Griscom and A. Sprunt, Jr., Eds.). New York, Devin-Adair Co.
- SKUTCH, A. F. 1967. Life histories of Central American highland birds. *Publ. Nuttall Ornithol. Club*, No. 7.
- SLUD, P. 1964. The birds of Costa Rica. *Bull. Amer. Mus. Nat. Hist.*, 128: 1-430.
- WETHERBEE, D. K. 1957. Natal plumages and downy pteryloses of passerine birds of North America. *Bull. Amer. Mus. Nat. Hist.*, 113:341-436.
- WETMORE, A. 1960. A classification for the birds of the world. *Smithsonian Misc. Coll.*, 139: 1-37.

Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana 70803. Present address: Department of Zoology, University of California, Berkeley, California 94720. Accepted 24 February 1970.