OBSERVATIONS ON THE NIGHTINGALE WREN IN COSTA RICA

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The Nightingale Wren (*Microcerculus marginatus*) is "famous both for its rarity in collections and the complicated series of plumages which have served as the basis of numerous supposed species" (Griscom, 1932a:360). The living bird is equally famous for its song, which has been highly commended by the few ornithologists who have heard it. Since there are few published references on the voice or habits of this bird, it seems desirable to present some of my observations made from 1950 to 1955 in the course of a general survey of the birds of Costa Rica.

DISTRIBUTION AND HABITAT

In Costa Rica, the Nightingale Wren lives throughout much of the country, almost exclusively in tall, virgin forest. Carriker (1910:754) gives its altitudinal range as extending from about 1500 feet to at least 7000 feet. I have seen the bird from a few feet above sea level up to nearly 6000 feet. The distribution of the bird's centers of abundance shows no particular correlation with the vertical zonation of climates. Thus, in southwest Costa Rica I found it common at upper tropical and subtropical elevations in the Térraba-El General region and at the foot of Mount Chirripó, and occasionally I noted its presence farther south in the lower tropical zone in the neighborhood of Piedras Blancas. On the Caribbean side of the country it is common low in the tropical zone in the extreme southeast, in the Talamanca-Sixaola region; to the north and west, the bird seems to be distributed locally in smaller numbers at various altitudes. In the northern half of the Pacific side of Costa Rica, it is absent from the relatively arid tropical lowlands, but it is a common resident above 2000 feet, along the wet, forested slopes of the continental divide where I even found it close to the summit of Miravalles Volcano. Depending upon the nature of the terrain, in many areas it seems to be restricted to steep slopes, ridges, and ravines, but in other places it may occur in comparatively level tracts (fig. 1).

It should not be inferred from the foregoing that this wren is one of the more common birds of Costa Rica. On the contrary, "common" is a relative term which I have applied to the bird's status in certain selected localities wherever one or more of several scattered individuals gives evidence of its presence at least once daily. In the El General region, for example, it is relatively so "common" that it may spread to the forest edge or beyond it into thickets and wild, scrubby growth. Nevertheless, the bird is rarely seen, and if it were not for its voice, it would escape detection almost completely.

A solitary bird, the Nightingale Wren dwells in brushy or leafy ground cover, where it often perches just above the forest floor. It is small in size (slightly over 4 inches), dark brown in color, with a diminutive, upturned tail and a rather long, slender, straight bill; even when seen it can be difficult to identify. It looks most like a small antbird of the semi-terrestrial type, particularly because of the stubby tail and, at close range, the bare bluish skin around the eye. This wren also resembles a small rail because of the tiny tail, long bill, and long legs. The dull coloration, although somewhat different from that of similarly plumaged birds, is of little comparative value in the obscurity of the forest understory.

This wren is difficult to find in spite of the fact that the call note betrays the bird's slow, steady progress through the undergrowth. It is most often met with accidentally, and the encounters are usually infrequent. An individual may halt its swift flight across a trail to perch sideways upon a stem before disappearing, or one might perhaps be glimpsed creeping into view upon a low limb or fallen trunk, or by chance it might be THE CONDOR

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spied upon the ground beside a pile of brush. This very peculiar wren, however, has the habit, when it walks, of teetering like a Spotted Sandpiper (*Actitis macularia*). Cherrie (1893:70) noted this mannerism and made the same comparison. If the observer will remember that the only other teetering birds in the Costa Rican forests are the Buffrumped Warbler (*Basileuterus fulvicauda*) and an occasional migrant water-thrush (*Seiurus motacilla* and *S. noveboracensis*) or Ovenbird (*Seiurus aurocapillus*), he will be able to identify this wren more readily.

VOICE

To some people in Costa Rica, especially in the northern half of the country, the bird is known, at least by reputation, as the "pito real." A small number of people have heard the song; even fewer persons can correctly associate the song with the bird producing it. Rarely, I have met someone who has been able to describe this wren as being very small in size, brown in color, nearly tailless, and ground dwelling.

Because of its name, one would expect that the Nightingale Wren is an accomplished singer. As attested to by Salvin (1861, 1866), Salvin and Godman (1880), and others, including myself, its voice is indeed remarkable. Identifying the sounds with the bird, however, is another matter. In my own case, I had to eliminate other species from consideration before suspecting that I had heard the Nightingale Wren. A longer period



Fig. 1. Map of Costa Rica showing localities where the Nightingale Wren (*Microcerculus marginatus*) was found. Dashed lines = 2000 meter contour; dotted lines = 1000 meter contour. Song types of Nightingale Wren are marked as follows: solid squares = "pito real" song; solid circles = the other song. Inset shows orientation in Costa Rica.

of time passed before I actually saw a bird singing. To complicate matters, this wren gives two songs which are completely different from one another. Thus, more time passed before I discovered that the second song also belonged to the Nightingale Wren.

Griscom's (1932b:299) statement that the bird has a marvelous song in the breeding season might imply that individuals sing only at that season. Unfortunately, this author does not tell us in which season the bird breeds. My records show that this wren sings throughout most of the year. I heard one of the songs in February, March, April, May, August, September, and November; the other song was heard in January, February, April, June, July, August, and the last week of October. I have no records for the missing months; at those times I simply did not happen to visit places where the birds occur.

The following "pito real" song is the one which Costa Ricans esteem and it is almost certainly the same as the song of Salvin and Godman's (1880:77) "ruiseñor" in Guatemala. The song is difficult to describe in other than generalized terms because it consists of individual, consecutively given whistles running into a pattern which rambles up and down the scale. If diagrammed, the song would look like a jagged graph. It starts with several high-pitched notes succeeding one another rapidly in ascending order, and then it slackens and trends irregularly downward and upward; suddenly it accelerates and rises in pitch until, having achieved a high point, it again sinks and fluctuates in random fashion, whereupon with renewed energy it mounts once more to a high, thin note of the musical scale. The high and low notes vary in the leisurely course of the long-continued, haphazardly sustained utterance. The penetrating quality of the notes is incisive rather than mellow, and the song as a whole, in my opinion, lacks sweetness. Although pleasing in a musical sense, it is not especially melodious. It is outstanding because of the striking, fitful variations in pitch, and the continually revived outpourings help make it totally unlike the song of any other Costa Rican bird. At a little distance, the high-pitched, rapidly rising sequences may not be heard but, even so, the rest of the song is instantly recognizable.

The other song is absolutely unique. It starts with three to eight rapid, thin whistles which, rising consecutively up the scale, are similar to those in the introduction to the song just described and in quality and pattern might be taken for a similar sequence given by the Cinnamon Becard (Pachyramphus cinnamomeus). The last of these thin whistles, however, is prolonged. It marks the close of the prologue and serves as the keynote for what follows. After a pause, the keynote is succeeded by another long, keen whistle that is slightly lower in pitch. A somewhat longer pause is followed by another sweet but "joyless" whistle which is fractionally lower in pitch, and so on. Each minor whistle, beginning with a lisp from which it emerges with a trace of an off-key quaver. follows the preceding one like a pensive afterthought. After the sixth or eighth whistle, the gradually lengthening intervals of silence may last up to ten seconds. By the time the twelfth or thirteenth whistle has been given, the fascinated listener has given up trying to predict whether the ensuing pause will eventually be broken by still another note, all the while wondering how much further the subtly altering pitch might succeed in its delicate descent. The song goes on, usually, for some thirty or forty notes over a period of several minutes. The listener is never sure when it has definitely reached its end. This simple song is the most remarkable one I know, but oddly enough few people whom I met in Costa Rica knew of this performance. Not many persons whose attention I directed to this song were visibly impressed by it. The song may sometimes be given in a slightly varied manner. With some individuals the pauses do not keep lengthening after the first several notes; with others, the notes may be doubled.

Wherever the Nightingale Wren occurs in the country, it may, or may not, give

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voice to a single long note, similar to a note in the song just mentioned, at intervals throughout the day. Often this note alone is sufficiently distinctive to indicate the presence of the bird in an area. It rather resembles the whistle of a Broad-winged Hawk (*Buteo platypterus*) when weakened by distance. The bird also gives a wren-like or antbird-like chatter, and a strong *stchep* (or *stchip* or *tseck*).

SONG AND TAXONOMY

A map, on which I have plotted the localities at which I heard either of the two songs, discloses a pattern of distribution that is as remarkable as the songs themselves (see fig. 1). This map shows that the "pito real" song was heard only in the northern half of Costa Rica, and that the other song was heard only in the southern half of the country. I have tentatively drawn the dividing line between the two zones as extending almost precisely along latitude $10^{\circ}N$, from Puerto Limón on the east coast to Puntarenas on the west coast. I know of no other bird in Costa Rica with such a pattern of variation. It violates all biogeographical boundaries.

I was first struck by this anomaly when I heard one song at the northern base of Turrialba Volcano and then heard the other song a little to the southeast of the same volcano. I could segregate other singing records likewise according to type. Although all records may each possess an equal value, it should be pointed out that these records were obtained in greater number in some localities than in others. In the northwest, southwest, and extreme southeast, I heard many birds over a large district; on the north side of Turrialba Volcano there seemed to be no more than one or two birds which I heard many times in a limited area. Elsewhere I heard only one bird singing once or, at most, two or three times. Nevertheless, the fact remains that not a single bird sang the "wrong" way. Each song represented a datum contributing to the establishment of this perplexing zonation.

Taxonomically, Ridgway (1904:667–670) believed that there were three nearly similar species of nightingale wrens in Central America: one in Guatemala, another in eastern Costa Rica, and a third from southwestern Costa Rica to the Isthmus of Panamá. Later, Bangs (1909:34–35), Hellmayr (1934:282–283), and Griscom (1932a:360–365) independently arrived at the conclusion that Ridgway's three species should be combined in a single subspecies. Griscom's investigation was particularly thorough. He examined no less than seventy-six specimens which were equally divided in number between Central American and South American forms. A study of "the exceptional material at [his] command" caused him to unite all the birds north of (and including) the Canal Zone into the subspecies *philomela* which he considered a race of the South American Microcerculus marginatus.

Neither Ridgway's treatment nor the treatments by Bangs, Hellmayr, and Griscom are in accord with the situation in Costa Rica as I have mapped it. The disagreement is caused by the conflict between an interpretation based on morphological grounds on the one hand, and geographic distribution based on song on the other hand. The fundamental question is: do differences or similarities in voice between closely related birds have taxonomic validity? In my opinion, this question must be answered in the affirmative with the qualification that the relative validity may differ from group to group.

If, with respect to song in the Nightingale Wren, the assumption is provisionally made that it does have some taxonomic value, a strange predicament results. As a consequence of this premise, the birds fall into neither specific nor subspecific categories, nor can they be regarded as subpopulations of a single race, as I shall attempt to show.

If two species of nightingale wrens should occur in Costa Rica, as Ridgway (1904) believed, then their geographical distribution fails to match the distribution of song

types. In order to conform to the latter, the birds of Caribbean Costa Rica (including those living along the continental divide in the northwest) must be split into a northern and a southern group, and this southern Caribbean group must be combined with the southwestern, Pacific group (fig. 1). If song is assigned the weight of a specific character, then Ridgway's assemblage of morphological specific characters breaks down when applied to either of the two groups segregated on the basis of song type. If the two song groups exhibited even the slightest constancy of morphologic characters in association with the differences in voice, they could conceivably be considered full species. In short, Ridgway's species, as redefined and reapportioned geographically on the basis of song, can no longer be characterized as species on morphological grounds.

Should song now be assigned the weight of a subspecific character, it can be used to test the view expressed by Bangs, Hellmayr, and Griscom. If there is in Costa Rica only one subspecies of Nightingale Wren, then this population must be considered as varying morphologically within narrow limits, since these systematists were unable to find consistent morphological characters by which to further subdivide the group. The dilemma is that the birds can be split into two contiguous geographic populations on the basis of song, thus implying the existence of two discrete groups, but these two groups cannot be differentiated by the museum taxonomist. In Costa Rica, there are definite instances of geographically separated races of other birds having dissimilar or completely different songs or calls consonant with the geographic ranges, but these races are characterized by morphological differences. On the basis of song, the taxonomic situation in the Nightingale Wren seems to be matched by no comparable one in the subspecific category.

As a final recourse, let the taxonomic weight of song be reduced still further to a position below the subspecific level. Local variations in bird songs do exist, and it is possible that one of these variations, at least when correlated with the limits of a geographically isolated group, may have a genetic basis, thus indicating a local population difference within the bounds of a morphologically defined subspecies. On the other hand, the song differences among the isolated groups making up a race may often be neither geographically correlated nor genetic but be due rather to imitative learning. However, unlike the song populations of other species of birds, those of the Nightingale Wrens of Costa Rica do not alternate geographically, nor are they randomly dispersed behind barriers so that an isolated group with one song type occurs within the range of birds with another song type. In addition, they do not present a situation in which a very small. local population occurs at the periphery of the range of a larger, more extensively distributed population. The division of the range in Costa Rica into a northern and a southern half is not duplicated for any other species in the bird fauna of that country. The distribution of song types affords no evidence of local population differences within either group.

From the preceding analysis, the conclusion is drawn that the Nightingale Wrens in Costa Rica, if not exactly deprived of a taxonomic status, are left with an indefinite one, and this suggests that in Central America the taxonomy of these wrens has not been definitely worked out. Further work is needed to resolve this problem. Fortunately, the living birds, by voice alone, offer in the field qualitative symbols capable of conversion into a quantitative pattern of distribution. Observations made at the southern limit of the range of *philomela* should be forthcoming from Barro Colorado Island in the Canal Zone, where many naturalists visit and where the bird has been known to occur and to sing (Eisenmann, 1952:1, 47). Information from the northern end of the range in Chiapas might be supplied by Paynter (1957a:270), who notes that this wren "was by no means rare" and that "its call is distinctive and was heard about once a day while collecting in the broadleaf forest."

If the wrens in a particular region should be determined as singing in the same manner, every specimen collected ought to have the song type marked on the label. As these specimens accumulate, a critical museum examination might yet manage to elaborate more detailed morphological criteria. A morphological recognition of two populations, in turn, could lead to a reappraisal of *philomela* and perhaps to a re-evaluation of the limits and contents of allied races.

DISCUSSION

The critical division between the song groups of the Nightingale Wren is, admittedly, distributionally irrational. Instead of coinciding with ecological barriers, it cuts across them. One might reasonably suspect that the birds were once separated and that their ranges adjoined later. The original separation could have been brought about, for example, "during the Cenozoic when Middle America was divided by various seaways," a possibility postulated by Paynter for his "*Troglodytes solstitialis* complex" (1957b: 13–14). If unqualified, this postulate ignores the element of time. A portal separating northern Central America from southern Central America existed from the early Paleocene to at least the mid-Pliocene (Simpson, 1950:365). Therefore, even if it be conceded that these ancient wrens had already attained the status of a recognizable entity in the Paleocene, until the reappearance of a land connection there intervened a temporal gap during which there was ample time for the groups to have evolved into unequivocally distinct, perhaps supraspecific, taxa. It is inconceivable that two populations should have maintained a similar morphology after having lived in isolation from one another for approximately 50 million years.

This difficulty can be overcome only if one resorts to the possibility of island hopping. This provides a means whereby the individuals of an ancestral stock might have crossed the water barriers considerably later in the Tertiary. That it must have served as the distributing agent even for some members of certain groups of land mammals cannot well be disputed. Yet the forest habitat and habits of Nightingale Wrens strongly suggest dispersal along ecologically suitable corridors rather than by the accident of rafting or by the birds' impulsive vagaries to set out in flight over open ocean.

I think it more likely that the present distribution poses a Pleistocene or late Pliocene problem in time. With the re-establishment of a continuous land connection, Nightingale Wrens from South America could have found their way into the Central American isthmus simply by following their habitat in pre-glacial and post-glacial times, and, perhaps by shuttling back and forth, in glacial times. Pleistocene isolation, caused by the effects of glaciation and the island-like disposition of the Central American mountain massifs, would have been relatively recent geologically and would correlate with the relatively small morphological differences among the races or to the morphologically indiscernible difference between the song populations. In detail these arguments, too, suffer the misfortune that the Nightingale Wrens do not seem to have been influenced geographically by what could have been, for other species, important historical factors. Altitudinally, the occurrence of either song type both in the uplands and lowlands invalidates a proposal favoring vertical differentiation. In addition, montane groups which might have been isolated could have been connected, as they are today, by birds occupying the intermediate elevations. Latitudinally, the Nicaraguan "break," separating a northern from a southern population, would seem to be the location of a natural zone of transition. According to my findings, there is no zone of transition but a sharp dividing line which, moreover, lies to the south, where it passes through the lowlands and the central highlands of Costa Rica. An encroachment by northern birds upon the northern half of Costa Rica, displacing the southern element farther southward, could explain, but rather unsatisfactorily, the position of the dividing line. Or, the extensive volcanic activity of the Pliocene and Pleistocene upon the central plateau of Costa Rica could have created a discontinuity, but the Nightingale Wrens would seem to have been the only birds so affected. The morphological similarity of the birds and the sharpness of the division between the two song populations remain unexplained.

The most important variation in these wrens seems to be in the songs. Starting with them, one can reason forward from, or backward to a time when the groups had become isolated, inconclusively, perhaps, as to the precise period or method of isolation; the finding of fossils would hardly clarify a situation for which singing birds are indispensable. Following the line of thought suggested by differences in voice, one can explore the possibility that song accounts for the present geographic distribution instead of placing emphasis upon the geologic events which might have governed the present distribution of song.

The Nightingale Wrens live in dark forest where they pursue their solitary ways low in the deep gloom of the undergrowth. The dull plumage seems to exhibit no adaptation other than to the surroundings. It is relieved by no bright areas or markings, and the bird flashes no mark, either hidden or exposed. If external morphology should play a passive part in recognition of one another by these wrens, minor variations might be retained, undiscriminated against by natural selection. As a matter of fact, Griscom has commented on the confusing array of taxonomically inconsistent plumages of philomela which he labored to fit to individual variation and, serially, to age (1932a:360). Hypothetically, on the other hand, a distinctive voice may first have been evolved for the sexual purpose of the birds' finding one another by sound, and perhaps also to deter a bird from intruding on territory already claimed. Next, a dichotomy in song type, resulting in a specialized development in each group, may have arisen after the parent population had become split into two groups. When eventually the ranges met, the different songs (which are apparently given the year round) could have acted as an isolating mechanism to prevent interbreeding. The boundary between the two song populations may represent this behavioral barrier-the chance meeting place to which the spreading front of either group happened to advance from an outlying center of dispersal.

CONCLUDING REMARKS

Perhaps the greatest significance to be attached to my observations is that they were made in the field and are based on behavior. Through one aspect of behavior, namely song, the taxonomic status of a race of the Nightingale Wren, presumed to be genetically uniform because of morphological uniformity, may have been reopened to question. How should other groups of wrens which show slight, or even prominent, morphological differentiation be treated? Most of the family Troglodytidae is notoriously difficult taxonomically at the racial, specific, and even generic levels.

Thus, Paynter (1957b:8-12), utilizing the evidence primarily provided by breeding behavior, synonomizes *Troglodytes brunneicollis* with *T. aëdon*, yet "lumps" *T. musculus* and *T. aëdon* despite the absence of such evidence. Further, solely on the basis of a morphological similarity, he has decided that the three groups of his "*Troglodytes solstitialis* complex" are conspecific (*op. cit.*:12-14). However, all three of these allopatric groups show decided behavioral differences. One member of the complex, *T. monticola*, according to Carriker (Todd and Carriker, 1922:418) "is a perfectly distinct, isolated species . . . confined to the Paramo Zone of the Sierra Nevada de Santa Marta . . . at elevations ranging from 11,000 to 15,000 feet, although it has not been detected below the latter altitude by the present writer." The other two members, *T. ochraceus* and *T*. rufociliatus, I have observed in luxuriant cloud forest in Costa Rica and Honduras respectively. Aside from the birds' unmistakably different appearance, their songs are quite different and their habits, arboreal in one and terrestrial in the other, are extremely different. In addition, Skutch (1940:307–308) has described the remarkable differences in nesting between ochraceus in Costa Rica and rufociliatus in Guatemala: the nest of ochraceus is built "in the decaying segments of branches or among the matted wefts of roots [of air-plants], hanging from the tree by a single stout root and swaying with every passing gust of wind... forty or fifty feet above the ground" where "these nests dangling free in the air ... are inaccessible;" the nest of rufociliatus "is an open cup ... placed in a narrow cranny in a trunk, near the ground, or else in a niche beneath an overhanging bank." Still another example is furnished by Campylorhynchus yucatanicus, listed as a subspecies of C. brunneicapillus by Hellmayr (1934:150), Blake (1953:399), and Paynter (1955:218), but considered specifically distinct on behavioral as well as on morphological grounds by Zimmerman (1957:57) and R. K. Selander (oral paper presented at A.O.U. meeting, Denver, 1956).

Song is but one of innumerable behavioral characters. Anything the living bird does is behavioral. When sufficiently pronounced, behavioral (and physiological) responses or traits can function effectively as isolating mechanisms when two similar populations meet. The degree of similarity, or of difference, between similar but geographically separated forms must be judged from as many lines of evidence as possible. It seems to be mandatory that the ornithologist have wide field experience, and it is the ornithologist with such background who is almost always conservative in his treatment of troublesome groups. I believe that the situation in the Nightingale Wren, aside from its own unique qualities, reflects the unsettled taxonomy of the Troglodytidae and points to the need for field observations. Song may reveal an unknown element in one instance, courtship displays may confirm a suspicion in another instance. Behavioral evidence can suggest the way to a more natural, systematized scheme of relationships after dead specimens have been exploited to the limits of the taxonomist's ingenuity and intuition.

SUMMARY

Observations on the habits and songs of the Nightingale Wren in Costa Rica are presented. Although only one subspecies of this wren, as defined morphologically, occurs in Costa Rica, two populations seem to be present, each characterized by a very distinctive type of song. The sharp line separating the northern song population from the southern one does not lie along any biogeographical boundary.

It is suggested that past geological factors cannot account adequately for the present distribution of these song populations. The well-defined differences in song may have arisen when the ancestral population was split into two isolated groups. When the isolating barrier disappeared and the two groups came together again, the differences in song may have acted as an isolating mechanism to prevent interbreeding between them. The line dividing the two groups at the present time may merely represent the chance meeting place to which the spreading front of either group happened to advance from an outlying center of dispersal.

Although the Nightingale Wrens of Costa Rica seem to be inseparable morphologically and are referable to a single subspecies on this basis, the presence of two sharply defined song groups in the population of Costa Rica indicates that the taxonomy of the species in that country, and perhaps in all of Central America, cannot be considered as definitely resolved. LITERATURE CITED

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