GEOGRAPHIC VARIATION AND SEXUAL DIMORPHISM IN THE TREMBLERS (*CINCLOCERTHIA*) AND WHITE-BREASTED THRASHER (*RAMPHOCINCLUS*)

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ABSTRACT.—I compared interisland variation in color and in length of wing, tarsus, and bill of the Lesser Antillean thrashers, *Cinclocerthia* and *Ramphocinclus* (Mimidae). Statistical analyses show that some early-taken specimens were missexed. I recognize two species of trembler, *Cinclocerthia ruficauda* (Brown Trembler) and C. *gutturalis* (Gray Trembler), and one of *Ramphocinclus* (White-breasted Thrasher). Brown Tremblers from Saba to Monserrat ("*C. r. pavida*") are not considered separable from those of Guadeloupe (*C. r. tremula*).

I summarize foraging methods and give possible explanations for the smaller amount of sexual dimorphism in bill length in *Cinclocerthia* on islands where *Ramphocinclus* occurs.
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THE avifauna of the West Indies is rich and well-known. Yet it has been underused as a source of information for zoogeographic and evolutionary studies. The Lesser Antilles, which extend in an arc south from the Virgin Islands toward Trinidad, are home to several endemic genera, including the tremblers (*Cinclocerthia*) and the White-breasted Thrasher (*Ramphocinclus brachyurus*).

Tremblers are long-billed, reddish brown or brownish gray thrashers found from the islands of Saba and St. Eustatius south to St. Vincent. At present, they are found primarily in wet, upland forests and less frequently in second growth (Bond 1936, American Ornithologists' Union 1983). In earlier classifications (e.g. Ridgway 1907), the grayish forms on Martinique and St. Lucia were both considered separate species. Current arrangements (Hellmayr 1934, Davis and Miller 1960) classify all the tremblers as a single species with six subspecies. From north to south, these subspecies are *Cinclocerthia ruficauda pavida* (Saba, St. Eustatius, St. Kitts, Nevis, and Monserrat), *C. r. tremula* (Guadeloupe), *C. r. ruficauda* (Dominica), *C. r. gutturalis* (Martinique), *C. r. macrorhyncha* (St. Lucia), and *C. r. tenebrosa* (St. Vincent). For reasons given below, the grayish tremblers of Martinique and St. Lucia are here considered a separate species, *Cinclocerthia gutturalis* (the Gray Trembler), and the reddish brown birds of the other islands are considered to be *C. ruficauda*, (the Brown Trembler). A fossil trembler is also known from deposits between 2,500 and 4,500 Y.B.P. on the island of Antigua (Steadman et al. 1984, Pregill et al. 1988).

The two forms of the White-breasted Thrasher have been considered separate species (Ridgway 1907), but they are currently considered conspecific (Hellmayr 1934, Davis and Miller 1960). They inhabit the adjacent islands of Martinique (*Ramphocinclus brachyurus brachyurus*) and St. Lucia (*R. b. sanctaeluciae*). Thus *Ramphocinclus* is everywhere sympatric with *Cinclocerthia gutturalis* whereas *C. ruficauda* occurs alone both to the north and to the south of the islands on which *Ramphocinclus* and *Cinclocerthia* are sympatric.

MATERIALS AND METHODS

I noticed both long- and short-billed birds in most of the populations of tremblers in the collections of the American Museum of Natural History. This difference was at least in part correlated with sex; the long-billed birds were usually sexed as females, and the short-billed birds as males. Data from this and other museums showed that there were apparent exceptions, especially among the specimens from Dominica whence seven short-billed birds were sexed as females and four long-billed ones as males (nearly one-fourth of the early-taken, sexed specimens from that island). Other preliminary data suggested that sexual dimorphism was reduced on Martinique and especially St. Lucia, where *Ramphocinclus* occurs with *Cinclocerthia*, so I examined and measured most available specimens of these genera.

Of the 391 specimens examined, 359 adults (280 of *Cinclocerthia* and 79 of *Ramphocinclus*) were used in the

analyses. This is not a large sample by modern standards, but it is so much larger than the series available to earlier reviewers (Ridgway [1907] reported on 61 specimens, and Hellmayr [1934], on 50) that, for the first time, variation within several of the populations can be treated statistically.

Measurements taken included wing length (chord), tail length, tarsus length, length of bill from the anterior border of the nostril, and culmen from the junction of the bill with the skull. Of these, wing length and length of bill from nostril proved the most useful; tail length was so greatly affected by wear that many measurements of it were useless; and bill length from skull proved difficult to duplicate. The ratio of wing length to length of bill from nostril was calculated for each bird.

Before I attempted an analysis of the variation among the populations, it was necessary to establish the extent of sexual dimorphism in *Cinclocerthia.* Although Ridgway (1907) reported sexual dimorphism in bill length, I found long-billed birds sexed as males and short-billed birds as females. This raised the question of whether these birds were missexed or whether individual variation in this genus is unusually large.

Missexed birds are probably more numerous in collections than is generally realized. They can be detected most easily in species with little or no overlap in one or more measurements (e.g. grebes; Storer and Getty 1985, Storer 1987). Because the males of most bird species have longer bills than the females, collectors probably missex more individuals of species like the tremblers in which the reverse is true.

I used the largest sample, 99 adult specimens from Dominica, for preliminary tests. Thirty-six birds from that island collected by Albert Schwartz in 1961 and 1962 yielded the following data: bill from nostril—24 males, 20.1–22.3 mm; 10 females, 23.7–27.5 mm; wing length/bill from nostril—23 males, 4.16–4.86; 9 females, 3.25–4.01.

Assuming that these birds were correctly sexed, I compared these data with the measurements of all the earlier-taken birds. The bill lengths of four older specimens (22.4, 22.4, 22.6, 23.3 mm) fell above those for males and below those for females in the Schwartz series. Of these, all but the third were well within the range of wing/bill ratios (4.32, 4.35, 4.12, 4.23, respectively) for males in the Schwartz series. All except the first bird (which was unsexed) were sexed as males by the collectors. The third bird is nearer to Schwartz's males than to his females in both bill length and wing/bill ratio. Therefore, I considered all four to be males. Four birds sexed as males were within the range of females in both characters and nine "females" fell within the range of males. A tenth bird sexed as a female had a bill for which bill-from-nostril measurement could not be taken but had a total bill length that was within the range of males and outside the range of females. Therefore, I considered all 10 birds to have been missexed.

I believe the assumption that birds were missexed is valid. First, there is a decided gap between the data for males and females in Schwartz's sample, and second, 10 of the 14 presumably missexed specimens were taken by two collectors, A. Hyatt Verrill (7) and Selwyn Branch (3). (Two birds taken in 1905, presumably by Verrill, came to the University of Michigan Museum of Zoology by way of the collection of Henry K. Coale, who removed the original labels and substituted his own. It is possible that Coale may have switched the labels, assuming that the longer-billed bird was the male.) On the other hand, Bond's (1952) questioning or discrediting many of Verrill's bird records from Dominica suggests that he was not a careful worker.

The preliminary results were tested further by obtaining discriminant functions for wing length, tarsus length, and bill from nostril for the Schwartz sample and using these to test the remaining birds from Dominica. In all cases, the results from the preliminary analysis were confirmed by discriminant-function analysis. A similar analysis was performed on the birds from Guadeloupe. The results indicated that a single female (MCZ 66485) was missexed. However, the bill length was within the range of females and outside the range of males for that population, whereas the measurements for wing and tarsus were within the range of both sexes. Because dimorphism is greatest in bill length and because there were no other individuals showing overlap, this bird was considered correctly sexed as a female.

I also tested the sexing of tremblers from St. Lucia by using discriminant functions. A single bird (BM[NH] 94.1.2.242, collected in February 1893) sexed as a female was classified as a male by discriminant-function analysis and was, therefore, considered missexed. The sexes of other birds I assumed to have been missexed or that I sexed on the basis of measurements were verified by this test.

A preliminary discriminant-function test for the Dominica sample on birds from St. Vincent showed that two Schwartz birds from the latter island might have been missexed. Discriminant functions calculated from the St. Vincent birds not collected by Schwartz were used to check the Schwartz sample, and the likelihood of missexing was confirmed. The bill measurements of these two birds, sexed as males, fell within the range of females. These birds were taken in February, when gonads are small and the chance of missexing most likely, so they were considered missexed. The sexes assigned to birds unsexed by the collectors and to birds believed to have been missexed are listed in Appendix 1.

After sexing was checked and corrected, I calculated means and standard deviations for each sex of the population of trembler on each island. Descriptive statistics for three combination of islands were also calculated: those traditionally included in the race *pavida* (Saba through Monserrat), the islands of St.

Eustatius, St. Kitts, and Nevis (which were probably connected at times of lowered sea levels in the Pleistocene), and the islands included in *pavida* plus Guadeloupe. Pairwise comparisons (Sheffe tests) were used to determine the significance of interisland differences. Dimorphism indices for each character of each island population were calculated as the difference between the means for the sexes divided by the mean for the means of the sexes and multiplied by 100 (Storer 1966).

Because of the large overlap in measurements between the sexes in the White-breasted Thrasher, I did not attempt to check for missexed birds or to assign sex to those unsexed by the collectors. Means and standard deviations for the sexed birds in both populations were calculated, as was the mean for the means of the sexes of both this species and the Gray Trembler on the two islands where they are sympatric. The last were used to calculate a species index in the same way as the dimorphism index was calculated.

In *Cinclocerthia*, there was no statistically significant relationship between the distance between islands and the amount of difference between populations on adjacent islands (comparing mean measurements for wing length, tarsus length, and length of bill from nostril for each sex independently with the interisland distances using a correlation matrix). The analysis was simplified because the islands lie along what is essentially a single axis.

Similarly, I used a correlation matrix to test for a statistically significant relationship between island size and each of the three linear measurements. Again, no such relationship was found.

A discriminant-function analysis was used to predict the percentage of specimens that could be identified on the basis of the lengths of wing, tarsus, and bill from nostril. This was performed for pairs of islands by sex. Discriminant functions were calculated for the three measurements for each island pair. Individual specimens were scored by multiplying their measurements by these functions and summing the products. These scores, based on the linear functions of the three variables, were used to calculate the predicted range of scores for each island. Individual scores were compared with the predicted range of scores for each island, and the number of specimens correctly or incorrectly classified was expressed as a percentage. I tested Monserrat vs. Guadeloupe, Guadeloupe vs. Dominica, Guadeloupe vs. St. Vincent, Dominica vs. St. Vincent, and Martinique vs. St. Lucia. Because of their very different coloration, the gray forms on Martinique and St. Lucia were not tested against any of the rufous forms.

The series of specimens from the Schwartz Collection (now at the Museum of Natural History, Louisiana State University), plus a pair of the Martinique Gray Trembler from the Field Museum of Natural History, were compared for color differences by R. C. Banks, J. W. Fitzpatrick, T. R. Howell, N. K. Johnson, B. L. Monroe Jr., H. Ouellet, J. V. Remsen, and the author.

Results

There are no clear trends in measurements of *Cinclocerthia*, from north to south (Table 1), nor is there a color cline. Sexual dimorphism ranges from ca. 2–5% for wing and tail length, is less (0.4–3.3%) in tarsus length, and is large (12.8–19.6%) in length of bill from nostril. The last is greatest in the three northern races, least in *macrorhyncha*, and intermediate in the other two. The index for wing/bill-from-nostril ratio is also least in *macrorhyncha* because of the small dimorphism index in bill length.

In *Ramphocinclus*, the Martinique race (*brachyurus*) is consistently smaller than that on St. Lucia (*sanctaeluciae*), and, except in culmen length, considerably less dimorphic (Table 1).

Tremblers from Saba, St. Christopher, Nevis, and Monserrat ("*pavida*") did not differ consistently in color. Birds from Guadeloupe (*tremula*) reportedly are darker overall and have grayer, less tawny, chests than "*pavida*" (Ridgway 1907). Although Schwartz's series from Guadeloupe is, on average, slightly darker than his series of "*pavida*," there is great overlap in this character; and the color of the underparts, including the chest, is quite variable, with nearly complete overlap between the Guadeloupe birds and those from the islands to the north.

According to Ridgway (1907), birds from Guadeloupe are dark like those from St. Vincent (*tenebrosa*) and thus darker than birds from Dominica (*ruficauda*). While the birds from Guadeloupe average darker above than those from Dominica, there is considerable overlap; and there is a nearly complete overlap in the color of the underparts.

Birds from St. Vincent are the darkest of the rufous populations. They are sufficiently deeper rufous on the back and darker gray on the crown and nape than the birds from Dominica to warrant subspecific recognition. Below, the St. Vincent birds average darker and tend to be more heavily marked with broad, diffuse streaks, but there is considerable overlap between the two populations in these two characters.

The Gray Tremblers from Martinique (*gutturalis*) and St. Lucia (*macrorhyncha*) differ markedly in overall color from the Brown Tremblers and differ consistently from each other in the

TABLE 1. Sample sizes, ranges, means, and standard deviations of measurements (mm) and dimorphism indices of the subspecies of tremblers and White-breasted Thrashers.

	Males				Females				Dimorphism index[1]
	n	Min–max	$\bar{x}$	SD	*n*	Min–max	$\bar{x}$	SD	
Wing length									
C. r. pavida	25	95.2–106.8	101.26	2.89	10	95.4–102.8	98.86	2.53	2.40
C. r. tremula	15	96.0–105.1	101.49	2.68	20	92.7–102.9	97.93	2.55	3.57
C. r. ruficauda	60	87.4–101.8	95.83	2.92	28	87.6–97.6	92.64	2.75	3.39
C. g. gutturalis	10	99.2–115.5	107.76	5.59	2	97.4–110.7	104.05	9.40	3.50
C. g. macrorhyncha	30	99.4–112.6	106.20	3.42	17	96.2–109.3	102.63	3.19	3.42
C. r. tenebrosa	23	93.1–101.3	97.19	2.22	18	87.6–97.6	92.68	2.84	4.75
R. b. brachyurus	16	91.3–102.3	96.11	3.77	9	89.4–105.0	95.67	4.33	0.46
R. b. sanctaeluciae	18	98.0–111.7	106.43	4.01	10	99.5–108.5	103.38	2.80	2.91
Tail length									
C. r. pavida	21	81.2–93.8	87.79	3.57	7	82.0–88.2	85.01	2.49	3.21
C. r. tremula	13	81.8–90.6	87.36	2.67	14	79.5–89.4	85.58	2.66	2.06
C. r. ruficauda	44	71.0–84.1	79.58	2.51	17	70.3–82.6	77.22	3.05	3.01
C. g. gutturalis	8	81.1–95.6	87.79	4.80	1	83.5			
C. g. macrorhyncha	20	80.0–94.5	87.71	3.74	10	78.3–92.5	85.18	4.06	3.93
C. r. tenebrosa	15	77.4–86.5	82.15	2.46	12	72.3–83.3	78.13	3.21	5.02
R. b. brachyurus	13	69.2–83.6	76.11	4.86	9	69.0–82.7	75.60	5.05	0.67
R. b. sanctaeluciae	14	77.5–92.5	85.11	3.71	8	76.4–86.9	81.44	3.71	4.41
Tarsus length									
C. r. pavida	31	29.5–32.9	31.29	0.90	12	29.4–32.9	30.83	1.09	1.48
C. r. tremula	20	30.1–34.9	31.61	1.15	21	29.9–33.3	31.49	0.84	0.38
C. r. ruficauda	62	27.3–31.2	29.25	0.77	27	26.4–30.9	29.06	0.85	0.65
C. g. gutturalis	9	31.5–34.3	32.76	0.94	1	29.3			
C. g. macrorhyncha	32	29.3–33.5	31.28	1.05	17	29.9–33.1	31.32	0.86	−0.13
C. r. tenebrosa	23	29.3–32.2	30.84	0.65	17	28.9–31.0	29.84	0.66	3.30
R. b. brachyurus	16	29.1–32.3	30.81	1.01	10	29.6–31.7	30.52	0.67	0.88
R. b. sanctaeluciae	21	32.6–36.0	34.26	0.92	11	31.1–35.4	33.59	1.68	1.97
Culmen length									
C. r. pavida	18	32.6–38.4	35.74	1.48	7	39.4–42.8	41.23	1.12	−14.27
C. r. tremula	6	33.7–36.6	33.47	1.04	11	38.6–44.6	41.68	1.86	−16.10
C. r. ruficauda	33	30.5–34.7	32.54	1.09	13	35.7–40.6	38.63	1.45	−17.11
C. g. gutturalis	3	34.1–37.5	35.47	1.80	1	39.5			
C. g. macrorhyncha	13	38.7–43.7	40.79	1.46	8	40.8–47.6	45.18	2.16	−10.21
C. r. tenebrosa	9	33.6–35.0	34.24	0.42	9	37.6–41.0	38.88	1.09	−12.69
R. b. brachyurus	9	27.3–30.7	29.22	0.99	5	26.0–28.6	27.58	1.06	5.77
R. b. sanctaeluciae	5	30.0–33.3	31.46	1.52	2	29.5–30.0	29.75	0.35	5.59
Bill from nostril									
C. r. pavida	32	21.2–25.6	23.35	1.09	11	26.5–30.0	28.18	1.01	−18.75
C. r. tremula	16	22.0–24.9	23.18	0.82	19	25.8–31.6	28.22	1.71	−19.61
C. r. ruficauda	60	19.7–23.3	21.28	0.76	28	23.7–27.6	25.89	1.05	−19.55
C. g. gutturalis	10	21.0–24.2	22.66	0.87	2	26.7–26.8	26.75	0.07	−16.56
C. g. macrorhyncha	29	25.1–30.2	27.62	1.27	16	29.7–33.6	31.38	1.31	−12.75
C. r. tenebrosa	20	21.2–23.7	22.40	0.62	17	24.8–29.0	26.35	1.16	−16.21
R. b. brachyurus	17	16.0–19.4	17.99	0.87	10	16.2–20.6	17.83	1.22	0.89
R. b. sanctaeluciae	20	18.2–22.0	20.08	1.00	11	17.9–21.2	19.51	1.04	2.80
Wing/bill									
C. r. pavida	25	3.9–4.9	4.37	0.27	9	3.2–3.7	3.50	0.14	22.11
C. r. tremula	12	4.0–4.7	4.36	0.22	19	3.1–3.9	3.50	0.22	21.88
C. r. ruficauda	58	3.5–5.0	4.50	0.24	27	3.3–4.0	3.59	0.19	22.50
C. g. gutturalis	10	4.2–5.4	4.73	0.31	2	3.6–4.2	3.90	0.36	19.24
C. g. macrorhyncha	27	3.6–4.3	3.85	0.17	15	3.0–3.5	3.28	0.16	15.99
C. r. tenebrosa	20	4.0–4.8	4.34	0.19	17	3.1–3.8	3.51	0.18	21.15

[1] Obtained by dividing the difference between the means for the sexes by the mean for the means of the sexes and multiplying by 100.

TABLE 2. Percentage separability of tremblers from pairs of islands, based on discriminant-function analysis of lengths of wing, tarsus, and bill from nostril.

Island pair	Percentage correctly classified		Color difference
	Males	Females	
Monserrat vs. Guadeloupe	62.5[a] vs. 58.3	100[b] vs. 83.3	+
Guadeloupe vs. Dominica	100 vs. 98.2	88.9 vs. 100	+
Guadeloupe vs. St. Vincent	100 vs. 100	83.3 vs. 94.1	−
Dominica vs. St. Vincent	87.7 vs. 95.0	80.0 vs. 64.7	+
Martinique vs. St. Lucia	100 vs. 100	100[b] vs. 100	+

[a] The pairs of figures are in the same sequence as those of the islands.
[b] Sample size = 1; all others ≥ 8.

color of the underparts as described by Ridgway (1907). The color differences between the two populations of the White-breasted Thrasher (*Ramphocinclus*) are also consistent and as described by Ridgway (1907).

While the Gray Tremblers differ most markedly in color from all the Brown Tremblers, they also differ more in color between themselves than do any two populations of the Brown Trembler. Discriminant-function analysis of measurements (Table 2) indicates that they also differ more from each other than do any pair of populations of the Brown Trembler in these characters.

DISCUSSION

A potential selective advantage to sexual dimorphism and an explanation for sexual differences in bill length may be related to foraging. In his work on the Brown Trembler on Dominica, Zusi (1969) found that these birds forage in a variety of ways. They take small fruits in trees and bushes, toss leaves to uncover small animals on the ground, probe in rotting logs, take small prey from crevices on tree trunks, or probe among tangled vines, clumps of dead leaves, or epiphytes.

Zusi believed the Brown Trembler's three most important potential competitors for food on Dominica to be the Scaly-breasted Thrasher (*Margarops fuscus*), the Pearly-eyed Thrasher (*M. fuscatus*), and the Forest Thrush (*Cichlherminia lherminieri*). The bills of these species differ markedly from those of the tremblers. The bill of the Scaly-breasted Thrasher is much shorter, and those of the other two (especially the Forest Thrush) considerably heavier. Zusi (1969) found other structural adaptations related to the trembler's arboreal foraging methods. The long bill and flattened cranium are related to probing narrow spaces, and the narrow antorbital region and the eyes are "oriented for close binocular vision." The short legs are "probably an advantage for perching on vertical surfaces." His comment that the reduced sternum and wings are "possibly correlated with the reduced need for extended flight" may be true, but the straight edge of the shallow, tapered keel of the sternum resembles that of woodpeckers and woodcreepers (Dendrocolaptidae) and may be an adaptation for bringing the center of gravity of the bird nearer to the substrate to which they cling. The specific advantage of this feature cannot be determined without a more detailed study of the bird's methods of locomotion, because Zusi's (1969) figure of a trembler clinging to a tree trunk shows the bird perched horizontally on the trunk rather than vertically like a woodpecker.

Zusi was unable to determine the sex of the birds that he watched foraging, so there is no information on foraging differences related to the sexual dimorphism in bill length. Speculation on this subject may provide hypotheses to be tested in future fieldwork.

The dimorphism in bill length is presumably related to differences in its use in probing, a method of foraging not shared with the trembler's potential competitors. The longer bill of the females increases the range of depths available to them and thus the potential for an increased feeding rate. This may be important for females when extra energy is needed for the development of eggs and during incubation, when foraging time may be limited. It might also be important if the female has the larger share in feeding the young, but the relative roles of the sexes in the care of the young are not known. The latter hypothesis does not,

however, explain why the males' bills are shorter. This may be related to a possible difference in the utilization of foraging places. Perhaps the males are better adapted for working in shallow crevices or foraging on the ground and the females for probing deeply in epiphytes. A foraging study with color-marked birds on Dominica, where the birds are still numerous, should answer this question.

On Martinique and St. Lucia, tremblers are much grayer than elsewhere, are less sexually dimorphic, and are sympatric with the White-breasted Thrasher, which is only known from these two islands. Competitive interactions between the two species are possible because the bill of the White-breasted Thrasher is more similar in shape to that of the trembler than any of the other sympatric thrashers or thrushes. At present, the numbers of both species are much reduced on both islands. In spite of the limited amount of overlap today, the earlier literature indicates that both species occupied a wider range of habitats before the islands were greatly modified by European settlers, and that they were probably sympatric over large areas.

On Dominica, where the mongoose (*Herpestes*) is absent and where Brown Tremblers are not uncommon today, they occupy a fairly wide range of habitats. Zusi (1969) found them in montane forests, secondary forests, and plantations, as well as rain forests, the most usual habitat on other islands, but he did not find them in dry scrub woodland during the leafless season. According to Diamond (1973), tremblers evidently occupy "a slightly wider range of habitats on St. Lucia than on Dominica," and Danforth (1935) found Gray Tremblers "locally common chiefly in the humid virgin forest, although found to some extent in second growth and in a low, rather dry, brushy type of forest." Bond (1928) found Gray Tremblers "a considerable distance from virgin forest . . . also in the low forest which peters out into arid scrub in northern St. Lucia." Zusi (in litt.) found both species along the Rivière Sourcière, St. Lucia, where White-breasted Thrashers were in bushes or feeding on the ground whereas Gray Tremblers were in taller, leafy trees or quite low in slender, scrubby trees. At this site he only observed tremblers foraging in dried leaves caught in a tree fork.

There is less information on the White-breasted Thrasher. Diamond (1973) says that "on both islands it now occurs only on scrub forests on the windward coast, showing a distinct preference for a low woodland with thin, crowded tree trunks, no ground cover and abundant leaf litter," and adds that it "feeds chiefly on the ground and mainly by turning over leaf litter," but that "one bird was seen to pick berries off a terminal twig." He continued that it "was formerly much more widespread, at least on St. Lucia, where Semper (1872) found it common." Semper (1872) only says that he met them "busily searching amongst the bushes near the ground and in low trees." According to his field notes for Martinique, Fred A. Ober (*in* Lawrence 1878) collected White-breasted Thrashers at Trois Islets and observed one in the Jardin des Plantes at St. Pierre. He commented that it "loves deep woods and the borders of streams." Near the mouth of the Rivière Chaloupe, St. Lucia, Zusi (in litt.) found White-breasted Thrashers both in spindly, short, deciduous trees 3–6 m tall and near or on a canyon floor where the trees were 18–21 m tall and greener.

From the above evidence, it appears that Gray Tremblers once occurred in the dry scrub forest where White-breasted Thrashers occur today and that the latter once occurred in deeper forest than they do now. Within the forests, the Gray Tremblers evidently foraged higher in the trees and the White-breasted Thrashers stayed on or near the ground.

The bill of the White-breasted Thrasher is much shorter and the cranium much higher than those of the tremblers (Zusi 1969). Presumably this limits the ability of these birds to probe in epiphytes or in crevices. The keel of the sternum in the White-breasted Thrasher is deeper and rounded in outline, unlike the shallow, straight-edged keel of the tremblers (pers. obs.). Presumably, the White-breasted Thrasher is less well-adapted for clinging to tree trunks than the trembler. On the other hand, it is relatively long-legged (wing/tarsus ratio 3.1 vs. 3.4 for the tremblers), indicating that it is a more terrestrial form, which is corroborated by Bond's statement (1957) that they "are largely terrestrial." Diamond's (1973) statement that they fed by turning over leaf litter, as Zusi (1969) reported Brown Tremblers did on Dominica, suggests that the White-breasted Thrasher may have taken over this feeding niche on Martinique and St. Lucia, "forcing" the tremblers on those islands to spend more time foraging in the trees. This is supported by Zusi's observations (in litt.) of White-breasted Thrashers' clearing small areas

of leaves by grasping and tossing, or by broom-sweeping with vigorous side-to-side sweeps of the bill, or by tossing to the front.

The difference in color between the Gray and Brown tremblers is not easy to explain. Some birds, like the Fox Sparrow (*Passerella iliaca*), show color differences that appear to be associated with habitat differences (Swarth 1920). The gray color of the tremblers on Martinique and St. Lucia may have resulted from a habitat difference, but if this is so it is difficult to explain on the basis of their present distribution, because the tremblers on these islands are now largely restricted to wet forests, the habitat in which they are most numerous on other islands. However, it may not always have been thus.

If dry scrub woodland was originally more extensive on Martinique and St. Lucia than on the other islands on which tremblers occur and if tremblers were numerous in this habitat, they might have been more easily seen by aerial predators such as barn-owls (*Tyto alba*) there than in the rain forest. Thus, the advantage of a grayish plumage in scrub woodland might have outweighed its possible disadvantage in rain forest. The darker, sooty color of the White-breasted Thrashers may be related to their spending much time in shadows on or near the ground.

White-breasted Thrashers are now birds of the scrub woodlands, and sexual dimorphism in the Gray Trembler is reduced on St. Lucia. These facts suggest the possibility that the White-breasted Thrasher, which has a similarly shaped but shorter bill, may have been more in competition with males than with the longer-billed females of the Trembler. Thus sexual dimorphism in the latter may have been reduced through a greater increase in the length of the males' than the females' bills.

An alternate hypothesis is that the Gray Trembler may have arisen on one of the low-lying limestone islands east of the volcanic arc on which Brown Tremblers now occur and later may have colonized Martinique and St. Lucia. Once there, it may have replaced an existing population of the Brown Trembler. A possible source of a gray ancestral stock is Barbados, where little original habitat is left and tremblers are not known to exist. The presence of a fossil trembler on Antigua is evidence that tremblers formerly occurred on low-lying islands of the limestone arc. The finding of such a fossil on Barbados would provide support for this idea.

It is possible that, like the Gray Trembler, the White-breasted Thrasher arose on the islands of the limestone arc and were successful in colonizing only Martinique and St. Lucia, possibly because the low scrub vegetation on these islands fit the ecological conditions of the islands on which they arose and to which they were adapted.

The original source of the White-breasted Thrasher is unclear. Although its juveniles are dark-breasted like those of tremblers, Zusi (1969) believed it nearest to the Mexican and Central American genus *Melanotis*, whereas *Cinclocerthia* may be distantly related to *Margarops* (including *Allenia*), the three species forming an endemic West Indian group, whose relationships with continental mimids remain to be determined. A genetic assay of these genera, their island populations, and their mainland relatives should prove most valuable in solving these problems.

Taxonomic Conclusions

The trembler forms *gutturalis* (Martinique) and *macrorhyncha* (St. Lucia) differ markedly from trembler populations on the other islands and to a lesser extent from each other. Both have been considered separate species (Ridgway 1907). Both are brownish gray rather than reddish brown in general color, but they differ from each other in details of the color of the underparts. The birds from Martinique average slightly larger in wing and tarsus lengths than those from St. Lucia, but the latter have much longer bills and are less sexually dimorphic in this character. The differences between these two populations and the rufescent ones are comparable to or greater than those between other pairs of thrasher species (e.g. the Brown Thrasher, *Toxostoma rufum*, and the Long-billed Thrasher, *T. longirostre*). In addition, Zusi (in litt.) found differences in vocalization and in trembling between the Brown Trembler on Dominica and the Gray Trembler on St. Lucia. On Dominica the tremblers were silent while foraging, whereas on St. Lucia they gave "a loud call of repeated notes when flying to another tree (the 'song' described by Bond [1936] as like a Carolina Wren's [*Thryothorus ludovicianus*]). Trembling differs in that, on St. Lucia, it is often confined to the tail." Evidence from the tapes of Roché (1971) and Hardy et al. (1987) further indicates vocal differences between the two

tremblers. I therefore recommend that they be separated from the other tremblers as *Cinclocerthia gutturalis* (Gray Trembler) and that the English name for the remaining populations be Brown Trembler.

The birds from the other islands (*C. ruficauda*) are more similar to each other in color and are separated primarily on the basis of measurements (Table 2). Populations from Saba to Guadeloupe do not differ sufficiently in measurements from island to island to warrant separation into subspecies. On the basis of color, birds from Guadeloupe (*tremula*) were formerly separated from those from the islands to the north (*"pavida"*) by their supposedly darker color and their grayer, less tawny or ochraceous chests, but these characters do not hold up in series. In spite of their being separated geographically by the two large, grayish forms on Martinique and St. Lucia, birds of the other two reddish brown races, *ruficauda* (on Dominica) and *tenebrosa* (on St. Vincent) are more similar to each other in size than to any other form. They average smaller than *tremula* including *"pavida,"* but they differ from each other in color, *tenebrosa* being darker in overall color.

Bangs (1929) described a race of trembler as *C. r. sola*, presumably from a small island off Guadeloupe. He claimed that it differed from the Guadeloupe form in being paler like *"pavida"* but had a much longer bill. I have examined the type and only specimen referred to the new subspecies in the Museum of Comparative Zoology. Its color is similar to that of a specimen in the same collection from St. Kitts. My measurements of the type are: wing 97.4 mm, tail 84.4 mm, culmen 41.9 mm, and bill from nostril 28.3 mm. The wing/bill-from-nostril ratio is 3.4. All are well within the range of females of *pavida* and *tremula* (cf. Table 1). In his description of *"sola,"* Bangs (1929) discussed the provenance of the unique type, the only paratype of *C. r. tremula* of Guadeloupe. He found the paratype so different from a series of specimens from Guadeloupe in coloration and bill length that he named it and said that it "probably [came] from some small island near Guadeloupe, possibly Desirade." Bond (1956), without presenting reasons, "suggested" Monserrat as the type locality. In view of the sexual dimorphism and considerable individual variation in coloration, which neither Bangs nor Bond recognized, and the agreement in measurements of the type of *"sola"* with females of *tremula* (including *"pavida"*), I think it possible that this specimen actually came from Guadeloupe. In any case, there seems to be insufficient evidence to assign any type locality to *"sola."*

Ridgway (1907) considered the two forms of the White-breasted Thrasher (*Ramphocinclus*) to be distinct species. They differ considerably in size and color. The St. Lucia birds (*sanctaeluciae*) are the larger in all measurements (Table 1), and the sides and flanks of the Martinique birds (*brachyurus*) are much paler than the upperparts, not the same shade as in the St. Lucia birds. More recent authors (Hellmayr 1934, Davis and Miller 1960) have considered the two conspecific.

While it is virtually impossible to determine if the species level has been reached between bird populations on adjacent islands, I believe that the relationships among the forms of these species are best represented by the following arrangement:

Cinclocerthia ruficauda tremula (including *pavida*)
Cinclocerthia ruficauda ruficauda
Cinclocerthia ruficauda tenebrosa
Cinclocerthia gutturalis gutturalis
Cinclocerthia gutturalis macrorhyncha
Ramphocinclus brachyurus brachyurus
Ramphocinclus brachyurus sanctaeluciae

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APPENDIX 1. List of unsexed specimens and those assumed to have been missexed and the sex assigned to each for the purpose of analysis in this paper.

Unsexed birds assumed to be males.—*Cinclocerthia ruficauda tremula*: AMNH 504515; FMNH 29046; MCZ 66489. *C. r. ruficauda*: MCZ 115101. *C. r. tenebrosa*: ANSP 160590. *C. gutturalis gutturalis*: FMNH 29053, 29055. *C. g. macrorhyncha*: FMNH 29073, 29076.

Unsexed birds assumed to be females.—*C. r. tremula*: FMNH 29044, 29047; ANSP 108764. *C. r. ruficauda*: BM(NH) 91.7.25.6. *C. r. tenebrosa*: FMNH 29060. *C. gutturalis macrorhyncha*: AMNH 504516; FMNH 29072.

Birds sexed as females, assumed to be males.—*C. r. pavida*: BM(NH) 40.5.13.3, uncatalogued; USNM 80954. *C. r. tremula*: MCZ 76365; ANSP 628. *C. r. ruficauda*: AMNH 406603, 504507; BM(NH) 89.6.10.8; FMNH 124862; MCZ 113588, 113589; ROM 339188; UMMZ 135042; YL 25559, 25563. *C. r. tenebrosa*: BM(NH) 98.2.8.26. *C. gutturalis gutturalis*: AMNH 174754, 748590; MCZ 76311; ANSP 9068; PA 1884218. *C. g. macrorhyncha*: AMNH 174753, 39222; BM(NH) 86.8.2.192, 94.1.2.242; CM 111640; MCZ 27381, 27382, 229536; USNM 80902.

Birds sexed as males, assumed to be females.—*C. r. pavida*: AMNH 174756; BM(NH) 91.1.25.2; ANSP 86438. *C. r. ruficauda*: FMNH 124861; ANSP 81191; ROM 22734; UMMZ 134382. *C. r. tenebrosa*: BM(NH) 98.2.8.25; SW 3307, 3310. *C. gutturalis gutturalis*: BM(NH) 86.28.2.190; ANSP 9067. *C. g. macrorhyncha*: BM(NH) 86.8.2.193; MCZ 29537, 29538.

APPENDIX 2. List of specimens examined and acronyms used for collections.

Specimens examined

Cinclocerthia ruficauda pavida. Saba (14): SW 7, USNM 4, ANSP 3. St. Eustatius (1): USNM 1. St. Christopher (10): SW 1, FMNH 6, USNM 1 (type), MCZ 1, BM(NH) 1. Nevis (10): SW 8, BM(NH) 2. Monserrat (10): SW 5, AMNH 1, USNM 4. *C. r. "sola."* "Guadeloupe" 1 (type): MCZ. *C. r. tremula*. Guadeloupe (50): SW 13, AMNH 7, FMNH 6, USNM 8, MCZ 10 (including type), BM(NH) 1, ANSP 1, PA 4. *C. r. ruficauda*. Dominica (99): SW 36, AMNH 12, FMNH 4, USNM 6, MCZ 6, BM(NH) 8, ANSP 3, YL 16, UMMZ 3, ROM 4, CM 1. *C. r. gutturalis*. Martinique (17): AMNH 3, FMNH 5, USNM 1, MCZ 1 (type), BM(NH) 2, ANSP 2, PA 3. *C. r. macrorhyncha*. St. Lucia (55): SW 16, AMNH 8, FMNH 7, USNM 5, MCZ 7, BM(NH) 5, ANSP 3, PA 1 (type), UMMZ 2, CM 1. *C. r. tenebrosa*. St. Vincent (41): SW 9, AMNH 5 (including type), FMNH 5, USNM 7, MCZ 4, BM(NH) 7, ANSP 4.

Ramphocinclus brachyurus brachyurus. Martinique (39): SW 10, AMNH 5, FMNH 5, USNM 3, MCZ 4, BM(NH) 6, ANSP 4, PA 2. *R. b. sanctaeluciae*. St. Lucia (44): SW 3, ANSP 6, FMNH 6 (including type), USNM 5, BM(NH) 5, ANSP 2, YL 6, PA 1, UMMZ 4, CM 1.

Acronyms used for collections

AMNH = American Museum of Natural History, New York City; BM(NH) = British Museum (Natural History), Tring; CM = Carnegie Museum, Pittsburgh; FMNH = Field Museum of Natural History, Chicago; MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts; PA = Paris Museum; ANSP = Academy of Natural Sciences of Philadelphia; ROM = Royal Ontario Museum, Toronto; SW = Collection of Albert Schwartz (now at the Museum of Zoology, Louisiana State University, Baton Rouge); UMMZ = University of Michigan Museum of Zoology, Ann Arbor; USNM = National Museum of Natural History, Washington, D.C; YL = Yale Peabody Museum, New Haven.