GENERAL NOTES

Wilson Bull., 96(1), 1984, pp. 91–99

Song variation and species discrimination in Blue-winged Warblers.—The ranges of Blue-winged (*Vermivora pinus*) and Golden-winged (*Vermivora chrysoptera*) warblers overlap extensively in the northeastern United States, and hybridization occurs frequently in areas of sympatry (Short, pp. 147–160 *in* Proc. 13th Internatl. Ornithol. Congr., Ithaca, New York, 1963). Information on singing behavior and interspecific discrimination of song has been obtained from populations of these two species in sympatry (Gill and Lanyon, Auk 81:53–64, 1964; Ficken and Ficken, Behaviour 28:149–181, 1967; Ficken and Ficken, Evolution 22:166–179, 1968a; Gill and Murray, Auk 89:625–643, 1972a; Gill and Murray, Evolution 26:282–293, 1972b; Murray and Gill, Wilson Bull. 88:231–254, 1976; Confer and Knapp, Kingbird 27:181–190, 1977), as well as from allopatric populations of blue-wings (Gill and Lanyon, 1964, Lanyon and Gill, Am. Mus. Novit. No. 2176, 1964; Ficken and Ficken, Wilson Bull. 81:69–74, 1969) and golden-wings (Ficken and Ficken 1969; Ficken and Ficken, Behaviour 46:114–128, 1973).

Both species have two song types, designated by Lanyon and Gill (1964) as Type I and Type II; the function of the two song types is uncertain. Both elicit a territorial response from males during playback experiments (Gill and Lanyon 1964; Ficken and Ficken 1969, 1973; Gill and Murray 1972b). Type I may also function in mate selection, but Type II usually is heard later in the breeding season, or after a territorial encounter has been initiated (Ficken and Ficken 1967; Ficken and Ficken, Wilson Bull. 80:442–451, 1968b; Gill and Murray 1972b). Kroodsma (Auk 98:743–751, 1981) provides evidence that local dialects exist in Type II song, but not in Type I song. Four basic components of blue-wing song have been described by Lanyon and Gill (1964) and Gill and Murray (1972b). Lanyon and Gill (1964) present evidence that Blue-winged Warblers from a Long Island population outside the range of golden-wings, exhibit much individual variation in the sequence and number of song components. Blue-winged Warblers in Michigan that are sympatric with Golden-winged Warblers have less variable songs (Gill and Murray 1972a).

Playback experiments have revealed that Blue-winged Warblers which live in sympatry with Golden-winged Warblers discriminate between blue-wing and golden-wing Type I songs better than do allopatric blue-wings (Gill and Lanyon 1964, Gill and Murray 1972b, Murray and Gill 1976). Discrimination between Type II songs of the two species is weak in both sympatry (Gill and Murray 1972b) and allopatry (Gill and Lanyon 1964). Gill and Murray (1972b) suggested that the reduced song variation in sympatric populations may have evolved to facilitate better interspecific discrimination, thus reducing the frequency of interspecific male-female sexual interaction, interspecific male-male aggressive encounters, or both. Alternatively, they note that differences between the sympatric Michigan populations and the allopatric Long Island population may result from chance divergence during allopatry, rather than an adaptive response to the presence of golden-wings in sympatry. My study was designed to distinguish between these alternatives.

Methods.—I studied seven New Jersey populations of Blue-winged Warblers daily, unless there was heavy rain, from 6 May–12 June 1980. I visited the populations on a rotating schedule to avoid biases which may result from comparisons at different stages of the breeding cycle. The study areas included one sympatric population of blue-wings and golden-wings near Waterloo Village (Morris County), and four allopatric populations of blue-wings: Hutcheson Memorial Forest (Somerset County), the Rutgers Ecological Preserve (Middlesex County), Herrontown Woods (Mercer County), and the Princeton Wildlife Refuge (Mercer County) (Fig. 1). Blue-wings and hybrids were present until 1980 in two other study areas,

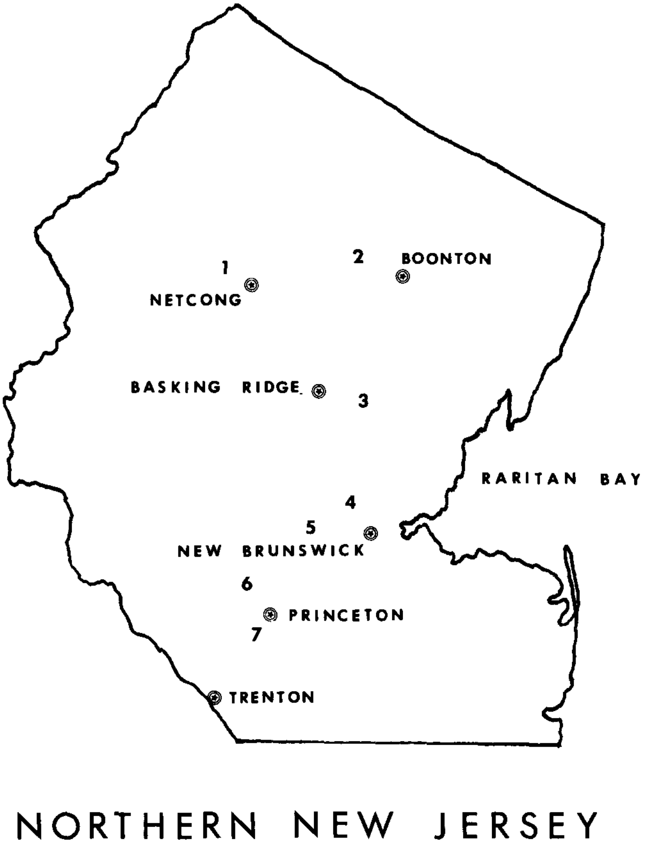

FIG. 1. New Jersey study areas. Number one represents the sympatric population; 2–3 represent the populations with hybrids; 4–7 represent allopatric populations.

located at the Great Swamp Wildlife Refuge and Troy Meadows (both in Morris County). The presence of hybrids in these two populations indicates that at least some of the individuals in the populations had had prior contact with Golden-winged Warblers, and that perhaps ancestors of the entire populations were sympatric with golden-wings at some time in the past. Throughout this paper, I will always refer to the Great Swamp and Troy Meadows as populations with hybrids, in order to maintain a distinction between them and the allopatric populations.

Based on an examination of museum specimens and historical records, Gill (Auk 97:1–18, 1980) hypothesized that Blue-winged Warblers became established in northcentral New Jersey approximately 50 years ago. The breeding range of the Golden-winged Warbler extends north of New Jersey, with a southern extension that coincides with the Appalachian Plateau (A.O.U. Check-list Committee, Checklist of North American Birds, 5th ed., Port City Press, Baltimore, Maryland, 1957). The sympatric study population and the two study populations with hybrids are located in or near northwestern New Jersey, which is part of

TABLE 1

PLAYBACK RESPONSE CATEGORIES AND SCORES

Response	Description	Score
Immediate	Approach to within 10 m of the playback area within the first six renditions	6
Delayed	Approach to within 10 m of the playback area after the first six renditions	3
Complete	Response continues throughout the 15 renditions	4
Active	Constant flitting about the playback area or the flicking of wings and tail of a perched bird	2
Study	Sitting almost motionless within 3 m of the tape recorder with occasional low-intensity vocalizations	2
Passes	Direct flight over the playback area	2
Silence	—	1
Muted song	—	1
Song resumption	Resumption of full song following termination of playback	2

the Appalachian Plateau. I found no record of golden-wings or hybrids breeding elsewhere in New Jersey. Although it is possible that Golden-winged Warblers have bred in areas where the four allopatric study populations of blue-wings are located, available evidence suggests that it is unlikely.

I tape recorded 574 Type I songs from 39 male blue-wings in the field, using a Uher 4000 Report IC tape recorder and a Bell and Howell directional microphone. I analyzed 234 songs (six per individual, in most cases) on a Kay Elemetrics Company Sonagraph Model 6061A. To determine the amount of individual variation, I measured the deviation about the central frequency and modulation rate of each song component. As defined by Greenewalt (Bird Song: Acoustics and Physiology, Smithsonian Institute Press, Washington, D.C., 1968) and modified by Gill and Murray (1972a), "central frequency" refers to the midpoint in the vertical distribution of energy shown on a spectrogram, and "deviation about the central frequency" refers to the range (i.e., the top and bottom points) of vertical energy distribution on a spectrogram.

I tested interspecific discrimination of song by performing playback experiments, similar to those performed by Gill and Murray (1972b). Individual males that sang Type I song within 60 m of the playback area were tested. Fifteen renditions of heterospecific song were played at 10-sec intervals, followed by 15 renditions of homospecific song. If there was a response to heterospecific song, the playback of homospecific song was delayed 10 min. If there was no response to heterospecific song, the homospecific song was played immediately. Responses were scored as described by Gill and Murray (1972b), and are summarized in Table 1. Seventeen was the maximum possible score. A response was considered "strong" if the total score of an individual was greater than 12, and "weak" if the total score was 12 or less. Individuals were placed in one of the following categories: (1) no response (no

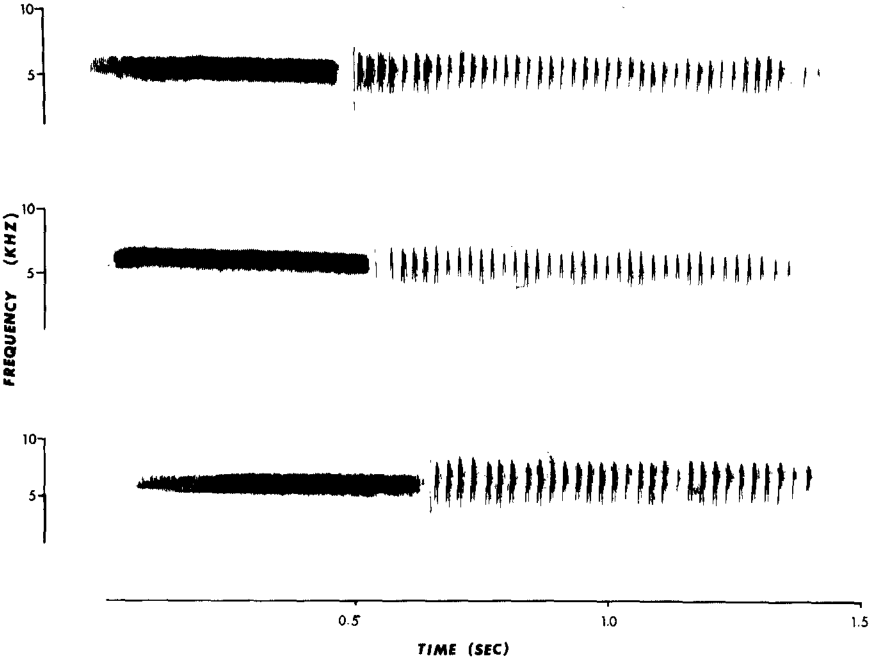

FIG. 2. Typical Type I songs (A-B Pattern) of Blue-winged Warblers. Top: recorded in a sympatric population; Middle: recorded in a population with hybrids; Bottom: recorded in an allopatric population.

response to heterospecific song); (2) weak response (weak response to heterospecific song); and (3) strong response (strong response to heterospecific song). Individuals that did not respond to homospecific song were not included in the analysis.

Results.—Thirty-six of 39 New Jersey blue-wings sang a typical A-B Song Type I (Fig. 2). Slight variation among males within a population occurs in modulation rate and deviation about the central frequency (Table 2). Since modulation rate usually varies within an individual song, I have presented high and low values which represent the range of variability. *F*-tests for homogeneity of variance revealed no significant differences among population types in these parameters (Table 2, $P > 0.10$ in all cases). The three aberrant songs (Fig. 3) were not associated with a particular population type. One was recorded from an individual in the sympatric population, and two were recorded from individuals in two different allopatric populations.

The seven New Jersey populations of Blue-winged Warblers exhibit less population variation in the number and sequence of song components, than was found in the allopatric Long Island population (Fig. 2; Lanyon and Gill 1964). The population variation in number and sequence of song components, deviation about central frequency, and modulation rate in all New Jersey populations is low and similar to the variation observed in Michigan populations (Table 2). *F*-tests for homogeneity of variance revealed significant differences

TABLE 2
VARIATION AMONG POPULATION TYPES IN TYPE I SONGS (A-B PATTERN) OF BLUE-WINGED WARBLERS

Song parameter	Population type			
	Michigan[a]	New Jersey		
	Sympatric (N = 16)	Sympatric (N = 7)	With hybrids (N = 13)	Allopatric (N = 19)
Component A				
MRL[b] (Hz)	229.4 ± 10.71 (4.0)[c]	230.0 ± 8.16 (3.6)	243.1 ± 12.51 (5.2)	235.5 ± 12.34 (5.2)
MRH (Hz)	242.5 ± 7.75 (3.0)	264.3 ± 7.87 (3.0)	265.4 ± 9.67 (3.7)	260.0 ± 10.26 (4.0)
FRL (kHz)	5.1 ± 0.25 (5.1)	4.3 ± 0.39 (9.2)	4.8 ± 0.39 (8.1)	4.6 ± 0.36 (7.7)
FRH (kHz)	7.1 ± 0.20 (2.9)	7.4 ± 0.38 (5.1)	7.5 ± 0.41 (5.4)	7.3 ± 0.57 (7.8)
Component B				
MRL (Hz)	44.0 ± 3.87 (8.9)	40.0 ± 0.00	40.8 ± 2.77 (6.8)	39.8 ± 1.12 (2.8)
MRH (Hz)	44.3 ± 4.17 (9.4)	45.7 ± 5.35 (11.7)	46.9 ± 4.80 (10.2)	45.0 ± 5.13 (11.4)
FRL (kHz)	3.7 ± 0.80 (21.4)	2.7 ± 0.39 (14.5)	2.9 ± 0.34 (11.8)	2.7 ± 0.49 (18.5)
FRH (kHz)	8.3 ± 0.46 (5.5)	8.7 ± 0.27 (3.1)	8.5 ± 0.43 (5.1)	8.7 ± 0.46 (5.3)

[a] Gill and Murray (1972a).

[b] MRL and MRH represent low and high extremes of the range of modulation rates. FRL and FRH represent low and high extremes of deviation about the central frequency.

[c] $\bar{x}$ ± SD (coefficient of variation).

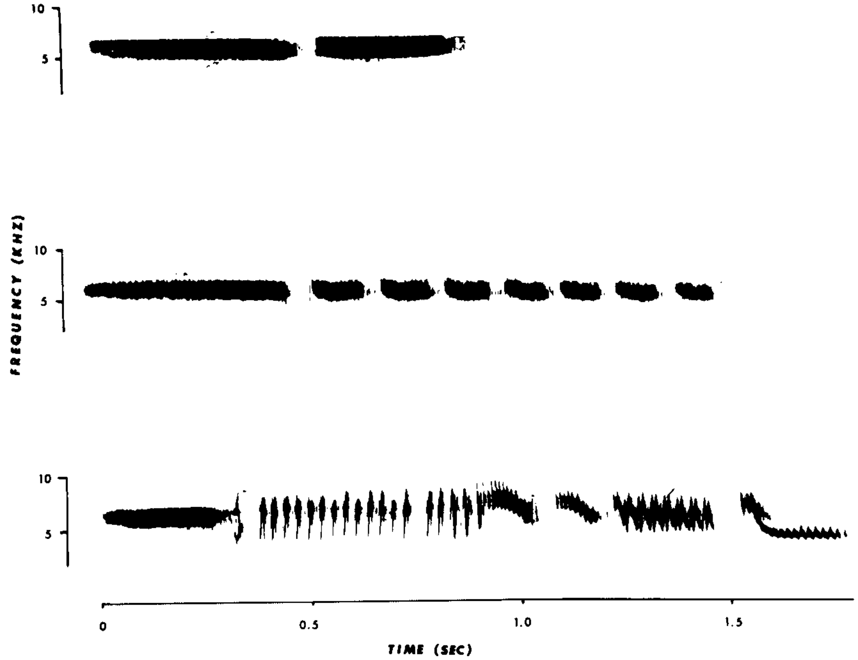

FIG. 3. Aberrant Type I songs of Blue-winged Warblers. Top and Bottom: recorded in allopatric populations; Middle: recorded in a sympatric population.

in only 3 of 24 comparisons between Michigan and New Jersey ($P < 0.05$, in all three cases): component A FRH was less variable in sympatric Michigan populations than in allopatric New Jersey populations; component B MRL was more variable in sympatric Michigan populations than in allopatric New Jersey populations; and component B FRL was more variable in sympatric Michigan populations than in New Jersey populations with hybrids. (Deviation about the central frequency and modulation rate were not measured in the Long Island songs.)

The behaviors of blue-wing males that responded strongly to the experimental playback of heterospecific song was similar to their behavioral responses to playback of homospecific song. A strong response usually included an immediate approach to the playback area, active behavior (a constant flitting about the experimental area or the flicking of wings and tail of a perched bird), direct flights over the tape recorder, silence or muted song, and resumption of full song after playback. The behavior of blue-wing males that responded weakly to heterospecific song differed not only in intensity but in quality. In 10 of the 13 cases of weak response, the warbler approached to within 10 m of the tape recorder during the first six renditions of playback, and sang throughout the experiment. The song was not muted or altered in any obvious way. Active behavior and flights over the tape recorder did not occur. Shortly after termination of playback, the male flew farther away and continued to sing.

Blue-winged Warblers sympatric with Golden-winged Warblers discriminated between blue-wing and golden-wing Type I songs more often than did Blue-winged Warblers from

TABLE 3
RESPONSES OF TERRITORIAL MALE BLUE-WINGED WARBLERS TO EXPERIMENTAL PLAYBACK OF GOLDEN-WINGED WARBLER SONG TYPE I

	No response	Weak response	Strong response	Total
Sympatric	4	2	0	6
With hybrids	4	3	2	9
Allopatric	5	8	4	17

allopatric populations; Blue-winged Warblers from populations with hybrids discriminated between blue-wing and golden-wing Type I songs more often than did blue-wings in areas where neither golden-wings nor hybrids have probably ever bred (Table 3, $\chi^2 = 12.65$, df = 1, $P < 0.005$).

Discussion. — Interspecific hybridization is expected to be maladaptive, occasionally acting as a selective pressure favoring increased premating behavioral isolation (Dobzhansky, Genetics of the Evolutionary Process, Columbia Univ. Press, New York, New York, 1970). Interspecific aggression is always maladaptive in a subordinate species and may be maladaptive in a dominant species, whether or not it is a result of misdirected intraspecific aggression (Murray, Ecology 52:414–423, 1971; Biol. Rev. 56:1–22, 1981). Therefore, factors which promote species discrimination would be favored in situations where either hybridization or maladaptive interspecific aggression is likely to occur. Similar reasoning is implicit in Gill and Murray's (1972b) hypothesis that reduced song variation observed in sympatric populations of Blue-winged and Golden-winged warblers in Michigan may have evolved to facilitate the increased interspecific discrimination observed in the same populations, relative to an allopatric population on Long Island (Gill and Lanyon 1964, Lanyon and Gill 1964). My data appear to be inconsistent with this hypothesis, as well as with an alternative hypothesis that the observed differences between Michigan and Long Island may result from geographic variation, rather than as an adaptive response to the presence of golden-wings.

The interpretation of the results concerning song variation in New Jersey populations depends on whether or not golden-wings were sympatric with the four allopatric populations of blue-wings at some time in the past. If golden-wings and blue-wings were previously sympatric throughout New Jersey, then the low amount of song variation could be interpreted as the result of selection to facilitate interspecific discrimination. If golden-wings have never bred in the four allopatric study areas (which available evidence suggests [A.O.U. Check-list 1957]), then the absence of consistent differences correlated with allopatry or sympatry among the New Jersey populations suggests that there has been no selection for reduced variability. The apparent absence of such effects could indicate either the absence of a significant selective pressure or that the amount of variability in song was insufficient for selection to operate. Considering the close proximity of New Jersey and Long Island, it is surprising that song characters in the New Jersey populations examined are more similar to song in Michigan populations. This suggests that the variation in Long Island song cannot be explained simply as geographic variation. The low amount of variation in allopatric New Jersey populations also indicates that the variation in Long Island song cannot be attributed to an absence or relaxation of stabilizing selection owing to an absence of Golden-winged Warblers. Further research will be necessary to determine why blue-wing songs on Long Island are so variable.

Although there is no difference in song variation among the New Jersey populations, Blue-winged Warblers that are sympatric with Golden-winged Warblers discriminate between heterospecific and homospecific song more often than do Blue-winged Warblers from allopatric populations (Table 3). Greater discrimination could result from selection to reduce the probability of hybridization, interspecific aggression, or both. Since only males respond to playback experiments, it is not possible to determine whether or not females follow the same trend in discrimination ability. Therefore, it is not possible to distinguish between the two selection pressures.

The greater discrimination observed in sympatric New Jersey populations could be genetically determined or learned. However, selection for genetically determined discrimination ability probably has not occurred in the New Jersey populations. Given the presence of hybrids at the Great Swamp and Troy Meadows, it is reasonable to assume that recent ancestors of many individuals in these populations had contact with golden-wings, hybrids, or both. If this assumption is correct, and if genetically determined discriminatory ability had been selected, individuals in these populations would be expected to discriminate as well as individuals from the sympatric population, because selection pressures probably would not have relaxed for sufficient time to produce a noticeable genetic change.

Gill and Murray (1972b) and Murray and Gill (1976) suggested a more plausible explanation for differences in discrimination ability based on learning. Blue-winged Warblers sympatric with Golden-winged Warblers could habituate (i.e., cease to respond) to interspecific song owing to a lack of appropriate visual stimuli. This does not require that the species be sympatric for a long period. The two populations with hybrids provide evidence for this hypothesis because they contain an intermediate number of discriminators. An intermediate number of discriminators could result if: (1) older birds learned to discriminate in previous years when there may have been greater numbers of golden-wing or hybrid models, while younger birds did not learn to discriminate because of fewer models or (2) the number of models in these populations has been consistently fewer than the number of models in the sympatric population, and only those blue-wings which had frequent contact with golden-wings or hybrids (e.g., neighbors with adjacent or overlapping territories) learned to discriminate.

In general, behavior patterns are triggered by any one of a broad range of stimuli. However, the intensity of the response will vary with stimulus intensity and quality. There is usually an "optimal" stimulus which will elicit the strongest response. For example, Curio (Animal Behaviour 23:1–115, 1975) has shown that the form and intensity of mobbing vary with the similarity between an experimental stimulus and an actual predator. Similarly, Blue-winged Warblers exhibit varying responses to a broad range of auditory stimuli. A typical Blue-winged Warbler in an allopatric population will respond by approaching a song of buzzy quality. Yet, the quality and intensity of the response to a golden-wing song differ from those exhibited in response to the optimal stimulus, blue-wing song. Inexperienced individuals in sympatric populations may show the same response. However, experience with golden-wings may eliminate the response by reducing the probability of responding to the sub-optimal stimulus of golden-wing song. Murray and Gill (1976) reported anecdotal evidence consistent with this view. A Blue-winged Warbler in a sympatric population initially responded aggressively to the song but not the plumage of a Golden-winged Warbler, that sang a blue-wing Type I song. Eventually, the response waned, although the individual continued to respond to other blue-wing songs, when associated with the appropriate visual stimuli.

A similar example of learning to modify a behavioral response based on an interaction between visual and auditory stimuli was reported by Rice (Wilson Bull. 93:383–390, 1981), who observed responses of Red-eyed Vireos (*Vireo olivaceous*) to a conspecific male which sang an aberrant song. Vireos which held territories distant to the aberrant individual ignored playback of the aberrant song, as if they did not recognize it as the song of a conspecific. However, the four immediate neighbors of the bird reacted to its song no differently than they reacted to normal song. Apparently the neighbors of this individual learned to respond to the unusual song because it was associated with the appropriate visual stimuli. The learning hypothesis could be tested by using models during playback experiments. If it is true, birds in allopatric populations should habituate to golden-wing song if it is presented simultaneously with a golden-wing model, but should not habituate if presented with a blue-wing model.

If it is adaptive for Blue-winged Warblers to discriminate between species (to reduce the frequency of hybridization, interspecific aggression or both), then the learning mechanism described here is probably more efficient than selection for a genetically determined response. Because selection for a genetically determined response involves a change in gene frequencies which varies with each situation, it requires more time and involves waste in maladapted offspring, whereas learning involves a rapid response to different environmental conditions and offers individuals immediate advantages (Shields, Philopatry, Inbreeding, and the Evolution of Sex, State Univ. of New York Press, Albany, New York, 1982).

Acknowledgments.—I wish to thank D. Caccamise, F. Gill, W. Lanyon, M. R. Lein, B. G. Murray, Jr., H. Power, and W. Shields for their critical reading of this paper. D. Caccamise generously supplied necessary equipment and instruction in use of the Sonagraph. M. Gorman and S. Peters provided valuable field assistance and creative ideas which increased my efficiency in the field. I am especially grateful to B. G. Murray, Jr., and W. Shields for their ideas and encouragement. The research was funded by a Sigma Xi Grant-in-Aid and a Frank M. Chapman Memorial Grant from the American Museum of Natural History.—JANICE R. CROOK, *Dept. Biology, Livingston Coll., Rutgers Univ., New Brunswick, New Jersey 08903.* (Present address: *Dept. Environmental and Forest Biology, State Univ. New York, Coll. Environmental Science and Forestry, Syracuse, New York 13210.*) *Accepted 15 May 1983.*

Wilson Bull., 96(1), 1984, pp. 99–103

The songs of *Microcerculus* wrens in Costa Rica.—The starting point of my recently published study of the taxonomy of *Microcerculus* in Middle America (Stiles 1983, Wilson Bull. 95:169–183) was the existence of two strikingly different "song types" in Costa Rica, as was first recognized by Slud (1958, Condor 60:243–251). Morphological and distributional data led me to conclude that the song types in reality represented different species, the northern *M. philomela* (Nightingale Wren) and the southern *M.* (*marginatus*?) *luscinia* (Whistler Wren). In the course of this study, I also recorded both song types, but unfortunately the sonograms reached me just too late to be included in the paper. Accordingly I present here descriptions and sonograms of representative songs of the two species of *Microcerculus* wrens in Costa Rica and briefly compared them with songs of other populations of these species, other *Microcerculus,* and other genera of wrens. Songs were recorded on a Uher 4000-L tape recorder with an M-517 Uher microphone and a Griffith fiberglass parabolic reflector.

The song of *M. philomela* (Fig. 1) consists of a long series of pure clear whistles, mostly without harmonics, that are given at a rate of ca. 2 per sec. The whistles are 0.3–0.4 sec in duration, and even-pitched or upslurred at frequencies between 3 and 6 kHz. Successive notes are typically on different pitches, such that the song "rises and falls in an arresting manner" (Slud 1958). The overall effect is sometimes strikingly tuneful, and was undoubtedly