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INTRODUCTION

THE NEED FOR A better understanding of specific limits within the flycatcher genus *Myiarchus* is especially acute for the insular populations of the West Indies. The lack of appreciable morphological divergence at the species level, heretofore the bane of those students who have attempted revisions in the genus, has been mitigated to some extent by recent studies involving populations in North and Middle America (Lanyon, 1960, 1961, 1963b, 1965) by the use of the color of the mouth lining and of spectrographic analysis of vocalizations. But even where divergence in morphology and voice can be demonstrated among the West Indian forms, how do we properly evaluate such divergence when denied the test of reproductive barriers to which we frequently resort when dealing with continental forms? Traditionally, differences between allopatric forms are judged in comparison with differences between congeners that do have an opportunity to interbreed, but this procedure has only limited value in difficult genera like *Myiarchus*. Fortunately, field experiments have demonstrated that differences in vocalizations function as the basis for species discrimination in several members of this genus (Lanyon, 1963a). When presented with a variety of vocal repertoires, through the medium of playback of sound recordings, a territorial male reacts positively only to that repertoire representative of its own species. In view of the lack of morphological divergence in these flycatchers, it is not surprising that selection should have favored divergence in vocal characters and a dependence on voice as an isolating mechanism. The ability of territorial males to discriminate between their own vocal repertoires and those of congeners from other islands, when sound recordings are played back simultaneously to simulate a condition of "sympatry," is the best index of reproductive isolation available for these insular forms.

The objectives of the present study were (1) to document the extent of divergence, in morphology and voice, between the various West Indian populations of *Myiarchus*; (2) to determine the specific limits within this

assemblage, based principally on the responses of territorial males to the playback of vocal repertoires; and (3) to attempt to reconstruct the evolution of these species, as newly constituted, and to determine their relative ages, origins, and paths of entry into the West Indies. The West Indies, as considered here, consists of the Bahamas and the Greater and Lesser Antilles south through Grenada, and including the Cayman Islands.

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The West Indian material at the American Museum of Natural History was examined and compared with specimens borrowed from the following institutions: Carnegie Museum, Pittsburgh; Field Museum of Natural History, Chicago; Peabody Museum, Yale University; and the University of Michigan Museum of Zoology. Dr. Albert Schwartz of Miami kindly sent me specimens to augment the comparatively small series generally available of the Lesser Antillean populations. Additional specimens were examined in the Academy of Natural Sciences of Philadelphia, the Institute of Jamaica in Kingston, the Museum of Comparative Zoology at Harvard University, and the United States National Museum of the Smithsonian Institution in Washington. I am grateful for the cooperation received from the curators of all of these collections. I am especially indebted to Mr. James Bond, with whom I had many fruitful discussions and considerable correspondence relating to both the planning of my field work and to the interpretation of my data. Mr. Peter Puleston accompanied me during the 1965 trip through the islands, as a participant in the Undergraduate Research Program of the National Science Foundation, and was a most helpful field assistant. Field work on many of the islands was greatly facilitated and in some instances entirely dependent upon the generous assistance and cooperation of local residents, notably Dr. James B. McCandless in Puerto Rico, Mr. Patrick J. Tenison in Jamaica, Mr. Stanley John in Saint Lucia, Mr. Bertil G. V. Owen in Saint Kitts, and Mr. P. G. C. Brudenell-Bruce in New Providence. Drs. William B.

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METHODS

The islands visited and the localities and dates worked are as follows:

NEW PROVIDENCE, BAHAMAS: Cultivated area and coppice between Lake Cunningham and Lake Killarney, April 17 to 21, 1963, and May 6 to 10, 1965.

GRAND CAYMAN, CAYMAN ISLANDS: Several localities, but particularly the clearings near the South West Point, May 15 to 19, 1966.

JAMAICA: Numerous localities in the eastern parishes, principally St. Andrew, St. Thomas, and St. Catherine, April 5 to 14, 1960; and the cockpit country of Trelawny Parish (Good Hope), April 8 to 17, 1963, and April 29 to May 6, 1965.

HISPANIOLA: Arid coastal country immediately north of Port-au-Prince, Haiti, May 9 to 15, 1966.

PUERTO RICO: Mayagüez, and the semi-arid deciduous and thorn woodland of Guánica Forest Reserve on the southwest coast, April 1 to 8, 1963, and April 22 to 29, 1965.

ST. KITTS: Forest clearings on the slopes of Mt. Misery, principally at 1500 feet on Molyneux Estate, April 15 to 22, 1960, March 29 to April 1, 1963, and April 17 to 22, 1965.

DOMINICA: Forest clearings on and near Springfield Plantation, Imperial Road, March 25 to 28, 1963.

MARTINIQUE: Semi-arid woodlands west of Ducos, April 22 to 25, 1960; near St. Anne, March 17 to 25, 1963; and southwest of Trois Ilets, April 8 to 16, 1965.

ST. LUCIA: Forest clearings near the summit of Piton Flore (above Forestière) and on the Marquis Estate east of Fond d'Assau, April 30 to May 7, 1966.

GRENADA: Semi-arid country of St. George and St. David parishes, March 13 to 17, 1963, and March 30 to April 6, 1965.

The procedure on each of these islands was to (1) locate as many territorial pairs of *Myiarchus* as possible, (2) obtain sound recordings of the vocalizations of these territorial birds, (3) observe breeding behavior and document nest sites whenever possible, (4) photograph the color of the mouth lining in fresh specimens or individuals that had been mist-netted, and (5) conduct standardized playback experiments to test the ability of territorial males to discriminate between their own repertoires and those of other populations.

Sound-recording equipment in 1960 consisted of a Magnemite recorder operated at 15 inches per second, a preamplifier, and an Altec 660B microphone mounted in a 24-inch parabolic reflector. In 1963, 1965, and 1966, the field recorder used was a Uher 4000 operated at 7.5 inches per second. Representative vocal patterns were then selected for analysis with a sound spectrograph. The spectrograms presented here were produced with the narrow band-pass filter, unless otherwise stated, and were chosen to demonstrate the extremes of variation evident for each population.

Close-up photographs of the color of the mouth lining of fresh specimens and live individuals were made with a Kodak Startech Camera equipped with a 1:1 accessory lens system, Ektachrome-X film, an 82A filter, and M3B flashbulbs.

Each of the playback experiments, which were conducted with those males exhibiting territorial behavior, consisted of dual sets of auditory and visual stimuli provided simultaneously. Standardized playback tapes representing the vocal repertoires of all the West Indian and North and Middle American populations of *Myiarchus* were prepared in advance to provide the auditory stimuli. These tapes were played back on two Uher tape recorders without additional amplification. Speaker cables permitted operation of the tape-drive equipment at 50-foot distances from two Electrovoice speakers set 75 feet apart. Two identical plastic models of the approximate size and color of a *Myiarchus*

flycatcher were positioned above the speakers to provide visual stimuli. No effort was made to vary the visual stimuli in these experiments, for previous experience with the North and Middle American species of *Myiarchus* had revealed that territorial males exhibit little, if any, visual discrimination (Lanyon, 1963a). Most of these experiments consisted of 16 minutes of playback of any two of the standard vocal repertoires, in combination with the two plastic models. After eight minutes of playback of the tapes, the cables of the two speakers were interchanged, so that during the remaining eight minutes the positional sources of the two sets of auditory stimuli were reversed from those of the first half of the experiment. Each experiment thus provided two opportunities to observe orientation by territorial birds to one or the other dual sets of audio signals: an initial orientation at the commencement of playback, and a second orientation following the interchange of speaker cables. Each of the experiments in Haiti, in 1966, were shortened to 10 minutes of playback, with a cable switch after five minutes. Notes were taken of the responses of the territorial birds, particularly with respect to their orientation or changes in orientation to one or both sets of speakers and models. A territorial bird was considered to have given a positive response to a particular repertoire if it oriented to within 30 feet of the plastic model and remained within that distance for all or nearly all of the eight-minute period during which the repertoire was emanating from the speaker associated with that model. For each positive response there was recorded a cor-

responding negative response to another repertoire associated with the second speaker and model. Each positive response could be classified further according to its intensity, i.e., whether the bird actively engaged in short flights in the vicinity of the model ("criss-crossing") or toward the model itself ("pass"), or perched within a few feet of the model ("study"), or actually made contact with the model (an "attack").

Museum specimens were examined and analyzed for morphological variation. Lack of adequate material in juvenal plumage has necessitated restriction of the definition of specific limits to adults (in plumages other than juvenal plumage). Linear measurements, in millimeters, were taken: wing, flattened; tail, from the insertion of the central rectrices; bill length, from the anterior margin of the nostril; bill width, at the anterior margin of the nostril. In the diagramming of statistical analyses (figs. 1-4), 1.3 times the standard deviation was plotted on each side of the mean (forming a solid rectangle). Thus, when two samples are compared, non-overlap of the solid rectangles indicates the probability that at least 90 per cent of the individuals of one population are separable from 90 per cent of the individuals of the other population with respect to the particular character that is analyzed.

The synonymies include the original description, the first usage of the principal combinations under which each name has appeared in the literature, and the names as they appeared in certain standard references (e.g., Ridgway, 1907; Hellmayr, 1927; Bond, 1956).

REVISION OF WEST INDIAN *MYIARCHUS*

OF THE 12 DISCRETE and recognizable forms of *Myiarchus* that are resident within the West Indies (Hellmayr, 1927; Bond, 1956), seven species (all endemic) are admitted on the basis of evidence reviewed here. No new forms are recognized, but I propose a substantially different definition of specific limits from the ones that have been advocated by other workers (see table 6). The morphological and vocal evidence for these taxonomic realignments is presented here, with the populations considered in a geographical sequence, beginning with the Bahamas and ending with the southernmost island of Grenada. The genus is represented on all the major islands in the West Indies and on most of the smaller ones, though there are no records for either Barbados or Antigua. Jamaica is the only island where more than one of these forms is found. The following key to the identification of these populations is offered in lieu of diagnoses and is applicable only to birds in definitive plumage. Text figures 1-4 and tables 1-5 should be referred to for measurements taken from samples studied.

KEY TO IDENTIFICATION

1. Abdomen white, or white with very pale yellowish wash 2
- Abdomen yellowish to bright yellow, never all white 4
- 2(1). Little or no cinnamon in tail; cinnamon normally confined to small areas at tips of inner webs; no prominent cinnamon stripe in any rectrix. Puerto Rico, Vieques, Culebra, St. Thomas, and St. John *antillarum* (p. 352)
- Prominent cinnamon in tail; not as above 3
- 3(2). No cinnamon in sixth rectrix, or cinnamon present as a very diffuse stripe in some individuals; prominent cinnamon stripe 3 to 5 mm. wide in rectrices 3 and 4, usually becoming diffuse in rectrices 2 and 5. Smaller; 90 per cent of the males may be expected to have the wing shorter than 86 mm. (52 males ranged from 78 to 87 mm.); 90 per cent of the females may be expected to have the wing shorter than 82 mm. (29 females ranged from 76 to 83 mm.). Cuba, the Isle of Pines, and Grand Cayman *sagrae* (p. 339)
- Cinnamon stripe in sixth rectrix usually present (in some cases absent), though frequently diffuse; prominent cinnamon stripe 3 to 6 mm. wide in rectrices 2 through 5. Larger; 90 per cent of the males may be expected to have the wing 86 mm. or longer (31 males ranged from 84 to 91 mm.); 90 per cent of the females may be expected to have the wing longer than 81 mm. (30 females ranged from 80 to 87 mm.). The Bahamas *lucaysiensis* (p. 335)
- 4(1). Smaller; wing (both sexes) shorter than 77 mm.; bill length (both sexes) shorter than 12.3 mm. No cinnamon in tail, or cinnamon limited to a stripe less than 1 mm. wide along edge of inner web. Bill wide in proportion to its length; bill length minus bill width less than 5.5 mm. Jamaica *barbirostris* (p. 342)
- Larger; wing (both sexes) 76 mm. or longer; bill length (both sexes) 12.2 mm. or longer. Cinnamon stripe in inner webs of rectrices wider than 1 mm. Bill not wide in proportion to its length; bill length minus bill width greater than 5.5 mm. 5
- 5(4). Cinnamon in tail restricted; no cinnamon in sixth rectrix, or else confined to small patch at tip of inner web or to a diffuse stripe along edge of inner web; sixth rectrix in no case with prominent, well-defined cinnamon stripe 3 mm. or more in width; cinnamon stripes on rectrices 2 through 5 often diffuse but may be prominent, up to 4 mm. wide 6
- Extensive cinnamon in tail; inner web of sixth rectrix almost invariably with a prominent cinnamon area that is nearly as wide as, or wider than, adjacent fuscous area; rarely (two out of 88 specimens), *dominicensis* may have the cinnamon pattern in the sixth rectrix diffuse 7
- 6(5). Bill narrower; width (both sexes) less than 7.3 mm. (47 specimens ranged from 6.5 to 7.2 mm.). Throat and chest pale gray (similar to *M. cinerascens* of western North America in this respect). Mouth lining pale orange in fresh specimens. Jamaica *stolidus* (p. 346)
- Bill wider; 7.2 mm. or wider (14 specimens ranged from 7.2 to 7.8 mm.). Throat and chest darker; light to medium gray (similar to *M. crinitus* of eastern North America in this respect). Mouth lining

- pale yellow in fresh specimens. Martinique *sclateri* (p. 356)
- 7(5). Fuscous in inner web of sixth rectrix confined to narrow stripe along distal half of rachis; proximal half of rachis of sixth rectrix bordered by cinnamon in inner web. Jamaica *validus* (p. 339)
- Fuscous stripe in inner web of sixth rectrix extending along entire length of rachis or at least along distal two-thirds of rachis 8
- 8(7). Smaller; wing length shorter than 90 mm. in males (54 specimens ranged from 79 to 89 mm.) and shorter than 87 mm. in females (34 specimens ranged from 76 to 86 mm.); females having a wing length of 85 or 86 mm. may be expected to have a bill width of 7.4 mm. or less. Hispaniola and offshore islands *dominicensis* (p. 349)
- Larger; wing length 90 mm. or longer in males and 85 mm. or longer in females; females having a wing length of 85 or 86 mm. (small *berlepschii*) may be expected to have a bill width of 7.5 mm. or more 9
- 9(8). Mouth lining (in fresh specimens) orange. Less cinnamon in the wing; most of the secondaries with leading edges fringed prominently with smoke gray or pale cream; presence of cinnamon confined to leading edges of primaries and occasionally the first and second secondaries. Grenada, the Grenadines, and St. Vincent. *nugator* (p. 359)¹
- Mouth lining (in fresh specimens) pale yellow. More cinnamon in the wing; most of the secondaries as well as the primaries with leading edges fringed with cinnamon or buffy cinnamon
- . . . St. Kitts, Nevis, Barbuda, *berlepschii* (p. 354) Dominica, Guadeloupe, *oberi* (p. 356) St. Lucia, *sanctaeluciae* (p. 359)²

***Myiarchus sagrae* (Gundlach)**

***Myiarchus sagrae lucaysiensis* (Bryant)**

Tyrannula stolidus (var. *lucaysiensis*) BRYANT, 1867a, p. 66.

¹ Worn specimens may not key out here, for the extent of cinnamon edging on the remiges, though a real character, becomes difficult to determine when the feathers are excessively worn.

² Three Lesser Antillean populations key out here. Properly sexed individuals can probably be separated with 80 to 90 per cent accuracy, using the mensural characteristics in tables 1-4 and text figures 1-4. All three forms have a pale yellow mouth lining, and there are no useful differences in plumage pattern or coloration.

Myiarchus sagrae lucaysiensis: RIDGWAY, 1907, p. 637 (synonymy).

Myiarchus stolidus lucaysiensis: HELLMAYR, 1927, p. 171 (synonymy). BOND, 1956, p. 108.

RANGE AND SPECIMENS EXAMINED: The Bahamas: Abaco (16), Andros (four), Grand Bahama (two), Green Cay (two), Inagua (four), New Providence (27), the "Bahamas" (six).

This Bahamian form is one of only three throughout the range of the entire genus that are white-bellied, the other two being *sagrae* of Cuba and *antillarum* of Puerto Rico. Varying significance has been attributed to this aberrant coloration, for *lucaysiensis* has been considered a race of *M. sagrae* by some workers and a race of *M. stolidus* by others. Hellmayr (1927) lumped all the non-Jamaican populations in the Greater Antilles with *stolidus* of Jamaica, thus obscuring relationships within the assemblage, and this treatment has been universally followed since.

The white abdomen and presence of prominent cinnamon areas in the tail are morphological characters that *lucaysiensis* shares only with *sagrae*. It is likely that this sharing of characters in common was the basis for Ridgway's (1907) treating these forms as conspecific. Though there is some overlap in measurements and in rectrix coloration of these geographically adjacent populations, most properly sexed individuals of *lucaysiensis* can be separated from *sagrae* by their larger size and more extensive areas of cinnamon in the tail (see key, p. 334, and text fig. 1). The mouth lining of *lucaysiensis* is pale yellow like that of *sagrae*, *antillarum*, and the populations of *M. oberi* in the Lesser Antilles, and unlike that of *stolidus* and *dominicensis*.

The vocalizations of *lucaysiensis* are illustrated in plate 22. A comparison of the sound spectrograms in plates 22 and 23 indicates that *lucaysiensis* has the same vocal repertoire as does *sagrae* of Cuba and Grand Cayman, thus confirming the close relationship suggested by morphological characters. The most significant feature of the vocalizations of *lucaysiensis* (and *sagrae*) is the absence of any unmodulated, prolonged whistle. As is shown below, the other Greater Antillean forms with which *lucaysiensis* and

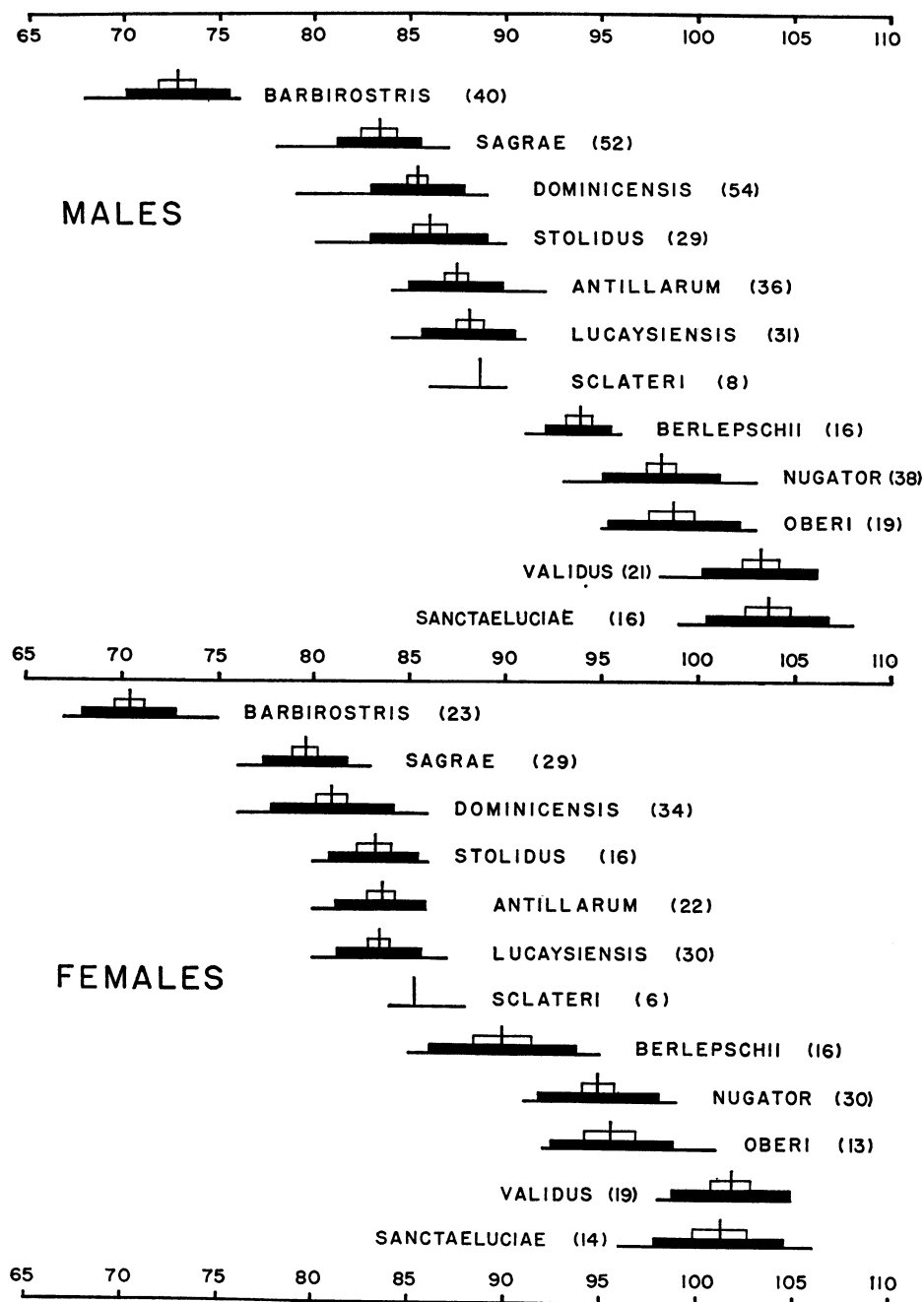


FIG. 1. Population-range diagram of the length of the wing, flattened and measured in millimeters, of *Myiarchus* flycatchers of the West Indies. Sample size in parentheses. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation.

sagrae have been allied by most workers are all "whistlers."

If the repertoire did, in fact, contain such a whistled note, experience with other "whistlers" in the genus tells us that we should expect to find such a note contained within the "dawn song", i.e., that assemblage of certain vocal patterns normally used during the daylight hours but rendered in a particular and characteristic sequence just prior to daybreak. The "dawn song" of *lucaysiensis* (pl. 22, figs. 1 and 3) consists of a combination of a modified "huit" note (pl. 22, fig. 5) and a rolling "brr-r-r" note (pl. 22, fig. 7), with no whistled element. The usual daytime vocalizations given by territorial individuals of *lucaysiensis* that are not excited or highly stimulated are the "huit" note and an occasional low-intensity, rolling "brr-r-r" note. With an increase in stimulation, the "huit" notes may be delivered in a series and with greater intensity (pl. 22, fig. 6), and the rolling note may be modified into sudden bursts of rapid oscillations which I call "rasping notes" (pl. 22, fig. 2). Most of the sound energy in the vocal repertoire of *lucaysiensis* is concentrated at about 4 kilocycles.

A total of 17 playback experiments were conducted on New Providence, involving three different territorial males. No nests were found, and I was unable to determine the breeding status of these experimental birds. All three of these males were able to discriminate between their own vocal repertoire and repertoires of *stolidus*, *antillarum*, and other congeners. At the time of these experiments, I had no recordings of *sagrae*, so was unable to test the reaction of *lucaysiensis* males to the vocalizations of *sagrae*. However, subsequent field work on Grand Cayman indicated that *sagrae* males are unable to differentiate between these two repertoires, which is what one would expect because their repertoires are identical spectrographically and to the human ear.

Descriptive notes taken in the field of a series of six experiments with one of the *lucaysiensis* males follow:

EXPERIMENT 130: May 7, 1965, New Providence, pair number 1. Tapes used, *lucaysiensis* versus *antillarum*; birds silent, location unknown

at start of experiment. Start at 6:47 A.M. Within 30 seconds, one bird appeared at 6 feet from *lucaysiensis* mount and then made a pass. Both birds criss-crossing at 6:49. In study at 2 feet from *lucaysiensis* mount. Both birds calling loudly. Repeated passes and criss-crosses within radius of 3-4 feet from mount at 6:53. Cable switch at 6:54. Both birds reoriented within 10 seconds after switch. Repeated passes and criss-crossing at new mount. 7:00, male still criss-crossing and passing at *lucaysiensis* mount. Very vocal. Female left area. Male remained, in excited passes at *lucaysiensis* mount. Strong response right up to end of experiment at 7:01.

EXPERIMENT 131: Same conditions as in experiment 130. Tapes used, *lucaysiensis* versus *stolidus* (but location of *lucaysiensis* speaker reversed from that at end of experiment 130); male within radius of 3-10 feet of old *lucaysiensis* mount at start of experiment. Start at 7:04 A.M. Within 15 seconds, male reoriented to new *lucaysiensis* area (leaving *stolidus* playback). Passes and criss-crosses, still very vocal. 7:06, male briefly went back to *stolidus* area, criss-crossed that speaker, but within 20 seconds was back criss-crossing *lucaysiensis* speaker. 7:07, male returned to *stolidus* area for 10 seconds, then back to *lucaysiensis* mount. 7:08, male criss-crossing *lucaysiensis* mount, calling well. Female showed at 7:09. Both in *lucaysiensis* area; male in study at 1 foot from mount, calling. Female left experimental area, male went to mid-point at 7:10. Male in a study at 2 feet from *lucaysiensis* mount at time of cable switch at 7:11. Male reoriented to new *lucaysiensis* mount within 5 seconds after switch. Criss-crossing and passes. At 7:12, male visited *stolidus* area briefly, then to mid-point, and back to *lucaysiensis* area. More passes and criss-crossing at *lucaysiensis* mount. Out of experimental area at 7:14, but back to *lucaysiensis* area in 30 seconds. Passes and criss-crossing. Briefly to *stolidus* area at 7:15, but then back to mid-point, and out of experimental area at 7:16. 7:17, back in *lucaysiensis* area, criss-crossing in radius of few feet of mount. End of experiment at 7:18.

EXPERIMENT 132: Same conditions as in experiment 130. Tapes used, *tyrannulus* versus *yucatanensis*; male silent in general area, 200 feet from experimental area, at start of experiment. Start at 7:25 A.M. Male under observation on tall, dead stub, 150 feet from each speaker. At 7:27, disappeared. No response. End of experiment at 7:32.

EXPERIMENT 133: Same conditions as in experiment 130. Tapes used, *stolidus* versus *nugator* [to test stimulus value of *stolidus* after no response in previous experiment]; birds silent, location unknown at start. Start at 7:37 A.M. No response. No vocalizing in area. At 7:41, male showed at

TABLE 1
WING LENGTH (IN MILLIMETERS) IN SAMPLES OF WEST INDIAN *Myiarchus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>lucaysiensis</i> (Bahamas)					
Males	31	84-91	88.1 ± 0.34	1.88	2.13
Females	30	80-87	83.5 ± 0.31	1.70	2.04
<i>sagrae</i> (Cuba, Grand Cayman)					
Males	52	78-87	83.4 ± 0.23	1.67	2.00
Females	29	76-83	79.6 ± 0.32	1.70	2.14
<i>stolidus</i> (Jamaica)					
Males	29	80-90	86.0 ± 0.43	2.34	2.72
Females	16	80-86	83.2 ± 0.45	1.79	2.15
<i>dominicensis</i> (Hispaniola)					
Males	54	79-89	85.4 ± 0.26	1.88	2.20
Females	34	76-86	81.0 ± 0.42	2.46	3.04
<i>antillarum</i> (Puerto Rico)					
Males	36	84-92	87.4 ± 0.31	1.87	2.14
Females	22	80-86	83.6 ± 0.39	1.84	2.20
<i>berlepschii</i> (St. Kitts, Nevis, Barbuda)					
Males	16	91-96	93.8 ± 0.34	1.34	1.43
Females	16	85-95	89.9 ± 0.74	2.96	3.29
<i>oberi</i> (Dominica and Guadeloupe)					
Males	19	95-103	98.7 ± 0.61	2.64	2.67
Females	13	92-101	95.6 ± 0.69	2.50	2.62
<i>sclateri</i> (Martinique)					
Males	8	86-90	88.6	—	—
Females	6	84-88	85.3	—	—
<i>sanctaeluciaae</i> (St. Lucia)					
Males	16	99-108	103.6 ± 0.61	2.42	2.34
Females	14	96-106	101.2 ± 0.71	2.64	2.61
<i>validus</i> (Jamaica)					
Males	21	98-106	103.2 ± 0.50	2.29	2.22
Females	19	98-105	101.8 ± 0.54	2.37	2.33
<i>barbirostris</i> (Jamaica)					
Males	40	68-76	72.8 ± 0.48	2.09	2.87
Females	23	67-75	70.4 ± 0.39	1.85	2.63
<i>nugator</i> (Grenada, Grenadines, and St. Vincent)					
Males	38	93-103	98.1 ± 0.38	2.37	2.42
Females	30	91-99	94.9 ± 0.44	2.43	2.56

same dead stub used during experiment 132. Called briefly. 7:43, male had moved to 50 feet of *stolidus* mount, but remained silent. Then moved to mid-point, silent. Cable switch at 7:44. Male disappeared, then seen again at the dead stub for a few seconds; disappeared again. No response to either tape in this experiment. End of experiment at 7:51. At 8:10, both birds responded well to playback of *lucaysiensis*, and the male was mist-netted close to the playback speaker (for purposes of photographing the color of mouth lining).

No further experimentation was made with pair number 1 until two days later.

EXPERIMENT 143: May 9, 1965. Same conditions as in experiments 130-133. Tapes used, *stolidus* versus *nugator* [no prior stimulation with *lucaysiensis* tape for two days]; birds in general area, calling sporadically. Start at 6:34 A.M. Male showed at 30 feet from *stolidus* mount, calling, within 15 seconds. Moved to 25 feet at 6:35, but remained silent. Moved out of experimental area at 6:38, called, and preened. No close approach. 6:39, male left general area, out of sight. Cable switch at 6:41. At 6:43, male appeared on dead stub about 60 feet from new *stolidus* model, silent, then disappeared again. No entry into experimental area. End of experiment at 6:48.

EXPERIMENT 144: Same conditions as in experiment 143. Tapes used, *lucaysiensis* versus *stolidus* [to test stimulus of *lucaysiensis* tape after negative response in previous experiment]; birds silent, location unknown at start of experiment. Start at 6:51 A.M. Male showed, 20 feet from *lucaysiensis* model, in 15 seconds, giving rasping notes and rolls. Moved to 15 feet, criss-crossing, study at 8 feet from *lucaysiensis* model. Moved to 5 feet, rasping notes, at 6:55. Criss-crossing, perch at 3 feet, study. 6:56, more criss-crossing. Moved briefly to 50 feet from *stolidus* model, but then back to 25 feet from *lucaysiensis* mount. Then to 20 feet from *lucaysiensis* model. 6:57, moved back to mid-point, silent. Moved to perch 70 feet beyond *lucaysiensis* model. Cable switch at 6:58, male reoriented at once to new *lucaysiensis* area, perching at 15 feet and very vocal. Then to 10 feet, and to 6 feet from *lucaysiensis* model at 7:00. Giving rasping notes. 7:02, moved over to 8 feet of *stolidus* model, stayed there for 20 seconds, then back to 10 feet from *lucaysiensis* model. Remained within 15 feet of *lucaysiensis* model until end of experiment at 7:05.

***Myiarchus sagrae sagrae* (Gundlach)**

Muscicapa sagrae GUNDLACH, 1852, p. 313.

Myiarchus denigratus CORY, 1886, p. 500.

Myiarchus sagrae sagrae: RIDGWAY, 1907, p. 636 (synonymy).

Myiarchus stolidus sagrae: HELLMAYR, 1927, p. 170. (synonymy). BOND, 1956, p. 107.

RANGE AND SPECIMENS EXAMINED: Cuba (56), Isle of Pines (20), and Grand Cayman (11).

Specimens from Grand Cayman (Cory's *denigratus*, 1886, p. 500) are not separable from Cuban specimens. That *sagrae* is closer, morphologically, to *lucaysiensis* than to any other population of *Myiarchus* is shown above. The two populations are nearly, but not completely, separable on the basis of wing length and rectrix pattern (see key, p. 334, and text fig. 1).

My field experience with this form has been confined to Grand Cayman, where I was able to determine that *sagrae* has a vocal repertoire and color of mouth lining identical to those of *lucaysiensis*, the white-bellied form in the Bahamas (see pls. 22 and 23). In view of the lack of any plaintive, whistled notes in the repertoires of *sagrae* on Grand Cayman and *lucaysiensis* in the Bahamas, I am puzzled by Chapman's observation (1892, p. 303) on the Cuban form: "It resembles a *Contopus* in habits, and its call has

the same plaintive quality as has the note of *Contopus virens*." This reference is the only one that I have found in the literature that related to the voice of the Cuban population of *Myiarchus*. I question that the Cuban form has a repertoire that differs in any way from that of the Grand Cayman and Bahamian birds, and suggest that Chapman may, in fact, have been unknowingly describing the voice of *Contopus caribaeus* which he also characterized as being "suggestive of those of *Contopus virens*" (*loc. cit.*).

Territorial males of *sagrae* on Grand Cayman responded positively to the playback of *lucaysiensis* recordings. In fact, only *lucaysiensis* recordings were used to attract *sagrae* males into mist-nets in order that photographs could be taken of the color of their mouth linings. No standardized playback experiments were conducted with *sagrae*.

***Myiarchus validus* Cabanis**

Myiarchus validus CABANIS, 1847, p. 351. BOND, 1956, p. 109.

Tyrannus crinitus (not *Muscicapa crinita* Linnaeus) GOSSE, 1847, p. 186.

Hylonax validus: RIDGWAY, 1907, p. 814 (synonymy). HELLMAYR, 1927, p. 187 (synonymy).

RANGE AND SPECIMENS EXAMINED: Jamaica (41).

Though there has never been any question as to the specific limits of this largest of the three Jamaican forms of *Myiarchus*, there has been some argument over its affinities at the generic and family level. Ridgway (1907) transferred *validus* to a monotypic genus *Hylonax* in the family Cotingidae, largely because of the tarsal scutellation. But the arrangement of the tarsal envelope is subject to considerable variation even within genera, as Ridgway (*ibid.*, pp. 328-329, 336), was well aware, and *Myiarchus* is one genus that illustrates the occasional deviation from the exaspidean tarsus that characterizes many of the tyrannids. Zimmer (MS) was impressed with the variation between a holaspidean and an exaspidean tarsus in several species of *Myiarchus*, and he therefore doubted the generic distinction of *validus*.

It is also possible that Ridgway may have been influenced by the suggestion of March (1863, p. 288) that the nest of *validus* sometimes differs in its location from that characteristic of other species of *Myiarchus* by

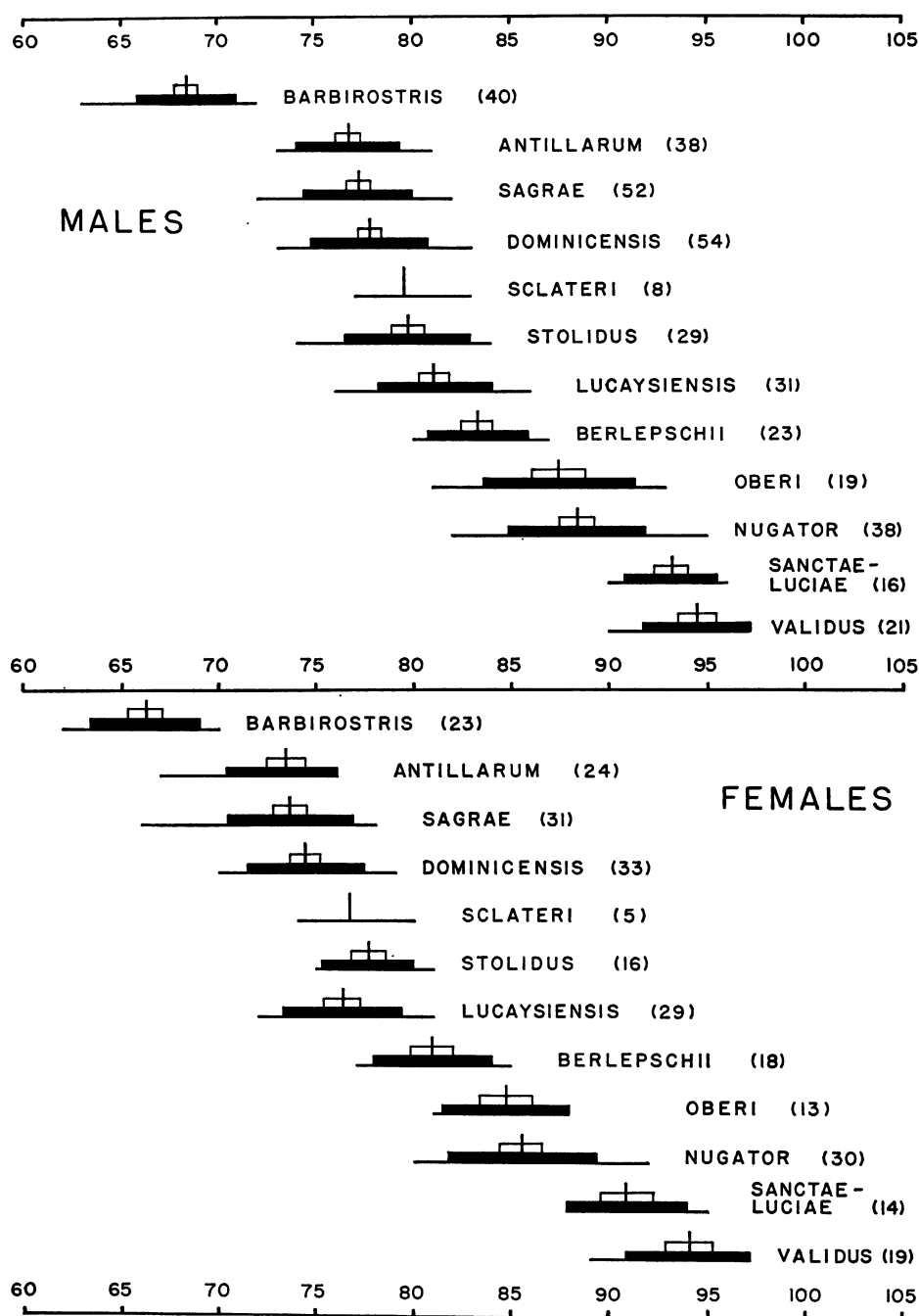


FIG. 2. Population-range diagram of the length of the tail, measured in millimeters, of *Myiarchus* flycatchers of the West Indies. Sample size in parentheses. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation.

TABLE 2
TAIL LENGTH (IN MILLIMETERS) IN SAMPLES OF WEST INDIAN *Myiarchus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>lucaysiensis</i> (Bahamas)					
Males	31	76-86	81.1 ± 0.41	2.26	2.79
Females	29	72-81	76.3 ± 0.44	2.36	3.09
<i>sagrae</i> (Cuba, Grand Cayman)					
Males	52	72-82	77.2 ± 0.30	2.18	2.82
Females	31	66-78	73.6 ± 0.44	2.45	3.33
<i>stolidus</i> (Jamaica)					
Males	29	74-84	79.7 ± 0.46	2.48	3.11
Females	16	75-81	77.6 ± 0.46	1.82	2.35
<i>dominicensis</i> (Hispaniola)					
Males	54	73-83	77.8 ± 0.31	2.28	2.93
Females	33	70-79	74.4 ± 0.40	2.29	3.08
<i>antillarum</i> (Puerto Rico)					
Males	38	73-81	76.7 ± 0.33	2.05	2.67
Females	24	67-76	73.4 ± 0.48	2.37	3.23
<i>berlepschii</i> (St. Kitts, Nevis, Barbuda)					
Males	23	80-87	83.3 ± 0.42	2.01	2.41
Females	18	77-85	80.9 ± 0.55	2.35	2.90
<i>oberi</i> (Dominica and Guadeloupe)					
Males	19	81-93	87.5 ± 0.69	2.99	3.42
Females	13	81-88	84.7 ± 0.71	2.56	3.02
<i>sclateri</i> (Martinique)					
Males	8	77-83	79.5		
Females	5	74-80	76.6		
<i>sanciae-luciae</i> (St. Lucia)					
Males	16	90-96	93.2 ± 0.45	1.80	1.93
Females	14	88-95	90.9 ± 0.64	2.38	2.62
<i>validus</i> (Jamaica)					
Males	21	90-97	94.5 ± 0.46	2.11	2.23
Females	19	89-97	94.1 ± 0.56	2.43	2.58
<i>barbirostris</i> (Jamaica)					
Males	40	63-72	68.4 ± 0.31	1.98	2.89
Females	23	62-70	66.2 ± 0.45	2.17	3.28
<i>nugator</i> (Grenada, Grenadines, and St. Vincent)					
Males	38	82-95	88.4 ± 0.44	2.69	3.04
Females	30	80-92	85.5 ± 0.53	2.93	3.43

being "placed in a fork or indentation or decayed hollow near the top of a tree; never in a deep hollow." But Bond (personal communication) has found the nests of this species to be situated in cavities or recesses similar to those sites selected by other species of *Myiarchus*, and my own field experience with *validus* supports this view. I agree with Bond's conclusion (1956, p. 109) that the "appearance, habits, notes and nidification [of *validus*] indicate that it is congeneric with *Myiarchus*."

Specimens of this endemic Jamaican species are readily separable from all other West Indian forms (see key, p. 335). The mouth lining of fresh specimens is bright orange, similar to that of *barbirostris* but richer than that of *stolidus*.

The most diagnostic vocal patterns of *M. validus* are illustrated in plate 24. Territorial *validus* are identified at once by the relatively short, piercing whistled notes (pl. 24, fig. 1) rendered at frequent intervals, interspersed with an occasional two-syllabled "wick-up"

call (pl. 24, fig. 2) or clicking note (pl. 24, fig. 6). With an increase in stimulation, the whistled note is modified and delivered in more rapid sequence (pl. 24, fig. 3) to produce a penetrating and emphatic roll (pl. 24, figs. 4 and 5). Most of the sound energy in the vocal repertoire of *validus* is concentrated from 3.0 to 3.5 kilocycles. No "dawn song" was heard, though the species undoubtedly possesses one.

Since this form occurs sympatrically with the other two species of *Myiarchus* in Jamaica and has no representative forms elsewhere in the West Indies, no standardized playback experiments were conducted with *validus*. In the course of obtaining recordings of *validus* repertoire, however, it was apparent that territorial *validus* males were very responsive to playback of their own vocal patterns and were not at all responsive to the repertoires of other congeners.

Myiarchus barbirostris (Swainson)

Tyrannula barbirostris SWAINSON, 1827, p. 366.

Myiobius tristis GOSSE, 1847, p. 167.

Blacicus barbirostris: SCLATER, 1871, p. 85.

Myiarchus barbirostris: CORY, 1892, p. 145. RIDGWAY, 1907, p. 652 (synonymy). HELLMAYR, 1927, p. 186 (synonymy). BOND, 1956, p. 109; 1964, p. 7.

Myiarchus tuberculifer barbirostris: BOND, 1957, p. 12; 1961b, p. 10.

RANGE AND SPECIMENS EXAMINED: Jamaica (65).

This smallest of the three Jamaican *Myiarchus* has no representative form elsewhere in the West Indies. Close relationship to *M. tuberculifer*, a successful and polytypic species of Middle and South America, was postulated by Ridgway (1885, p. 571) in a discussion of his "*M. platyrhynchus*" (= *M. tuberculifer platyrhynchus*) of Cozumel Island: "this bird is so closely related to *M. barbirostris* of Jamaica that it should perhaps be considered merely a local race of it." Zimmer MS, July 3, 1951) wrote of *barbirostris*: "Certainly a member of the *tuberculifer* group. It is small and rather pale below, but does not show any positive specific characters. In various respects it approaches *platyrhynchus* of Cozumel Island." Zimmer (MS) treated *barbirostris* as a race of *tuberculifer*, and this practice was followed by

Bond (1957, p. 12; 1961b, p. 10), though the name *barbirostris* has priority (as subsequently clarified by Bond, 1964, p. 7). I argue in the present paper that it should be treated as a monotypic species, endemic to Jamaica.

Specimens of *barbirostris* are separable from all the recognized races of *M. tuberculifer*. When compared with the Mexican members of this wide-ranging continental species, *barbirostris* is closest to *platyrhynchus* of Cozumel and the Yucatán Peninsula, but averages smaller in size and has a darker pileum and browner upper parts. The mensural character providing the least amount of overlap between *barbirostris* and *platyrhynchus* is bill length (see table 5). The Jamaican form is readily separable from the Central American representatives of *M. tuberculifer* (*connectens*, *littoralis*, *nigricapillus*, and *bangsi*) by the absence of the prominent cinnamon edging to the remiges, rectrices, and wing and tail coverts that is so characteristic of those forms. The four representatives of northern South America (*brunneiceps*, *pallidus*, *tuberculifer*, and *clarus*) have distinctly greener upper parts (less brown) than *barbirostris*.

The mouth lining of *barbirostris* is bright orange, thus agreeing in color with fresh specimens of *M. tuberculifer* that I have seen throughout Mexico and Central America.

In view of the undeniable morphological affinity of *barbirostris* and *M. tuberculifer*, a comparison of the vocal repertoires of these forms becomes especially important. There are certain obvious similarities of portions of their respective repertoires (see pls. 25 and 26) which support the morphological evidence of a close affinity. The single "huit" or "pit" note of these two forms (pl. 25, fig. 3, and pl. 26, fig. 5) are nearly identical, though that of *M. tuberculifer* may be slightly sharper and more emphatic to the human ear. When this note is delivered in a rapid sequence, it becomes a roll, which both forms possess (pl. 25, figs. 4 and 8, and pl. 26, fig. 1). Each of these repertoires also contains a rasping note (pl. 25, fig. 7, and pl. 26, fig. 7) and a two-syllabled "wick-up" note (pl. 25, figs. 5 and 6, and pl. 26, figs. 6 and 8) which are quite similar spectrographically and indistinguishable to the human ear.

TABLE 3
BILL LENGTH (IN MILLIMETERS) IN SAMPLES OF WEST INDIAN *Myiarchus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>lucaysiensis</i> (Bahamas)					
Males	31	14.0–15.9	15.00 ± 0.09	0.51	3.40
Females	30	12.5–15.3	13.93 ± 0.11	0.58	4.16
<i>sagrae</i> (Cuba, Grand Cayman)					
Males	50	12.9–15.6	14.36 ± 0.07	0.53	3.68
Females	30	12.6–14.8	13.41 ± 0.10	0.55	4.10
<i>stolidus</i> (Jamaica)					
Males	29	12.4–16.0	14.28 ± 0.14	0.73	5.11
Females	17	13.0–15.1	13.83 ± 0.13	0.52	3.76
<i>dominicensis</i> (Hispaniola)					
Males	51	12.9–16.3	14.52 ± 0.10	0.70	4.82
Females	34	12.4–15.3	13.63 ± 0.13	0.73	5.36
<i>antillarum</i> (Puerto Rico)					
Males	38	13.6–15.8	14.42 ± 0.09	0.54	3.74
Females	23	12.7–14.5	13.54 ± 0.10	0.48	3.55
<i>berlepschii</i> (St. Kitts, Nevis, Barbuda)					
Males	22	15.0–17.2	16.05 ± 0.12	0.58	3.61
Females	18	14.6–16.0	15.34 ± 0.11	0.48	3.13
<i>oberi</i> (Dominica and Guadeloupe)					
Males	18	15.2–18.1	17.17 ± 0.19	0.79	4.60
Females	13	14.6–17.6	16.52 ± 0.20	0.73	4.42
<i>sclateri</i> (Martinique)					
Males	8	13.8–16.6	15.39		
Females	6	14.2–15.8	14.60		
<i>sanctaeluciae</i> (St. Lucia)					
Males	16	17.4–20.1	19.02 ± 0.16	0.64	3.36
Females	13	15.9–19.4	18.18 ± 0.26	0.93	5.12
<i>validus</i> (Jamaica)					
Males	19	15.8–18.1	16.99 ± 0.14	0.59	3.47
Females	20	15.8–17.8	16.89 ± 0.13	0.58	3.43
<i>barbistrois</i> (Jamaica)					
Males	38	10.3–12.3	11.41 ± 0.08	0.49	4.29
Females	21	10.2–11.9	11.08 ± 0.11	0.51	4.32
<i>nugator</i> (Grenada, Grenadines, and St. Vincent)					
Males	37	16.1–18.4	17.34 ± 0.10	0.62	3.58
Females	30	16.0–18.0	16.80 ± 0.09	0.52	3.10

Even the "dawn songs" show obvious similarities in that both forms characteristically render whistled notes and prolonged rolls just before daybreak (pl. 25, figs. 1, 2, and 8, and pl. 26, fig. 1).

The presence of a whistled component in the "dawn song" of *barbistrois* is especially interesting and somewhat paradoxical, for this Jamaican form has no such whistled note in the vocal repertoire that it uses during the daylight hours. During my three visits to Jamaica I had the opportunity to

make notes and sound recordings of the vocalizations of 19 pairs of *barbistrois*, all territorial and highly vocal. None of these birds was ever heard to render the prolonged whistled note that is given so frequently and characteristically by *M. tuberculifer* throughout its extensive range (pl. 26, figs. 2–4). Discussions with other observers who have had field experience with this Jamaican bird have confirmed this point.

Those members of the genus that can be characterized as "whistlers," by virtue of

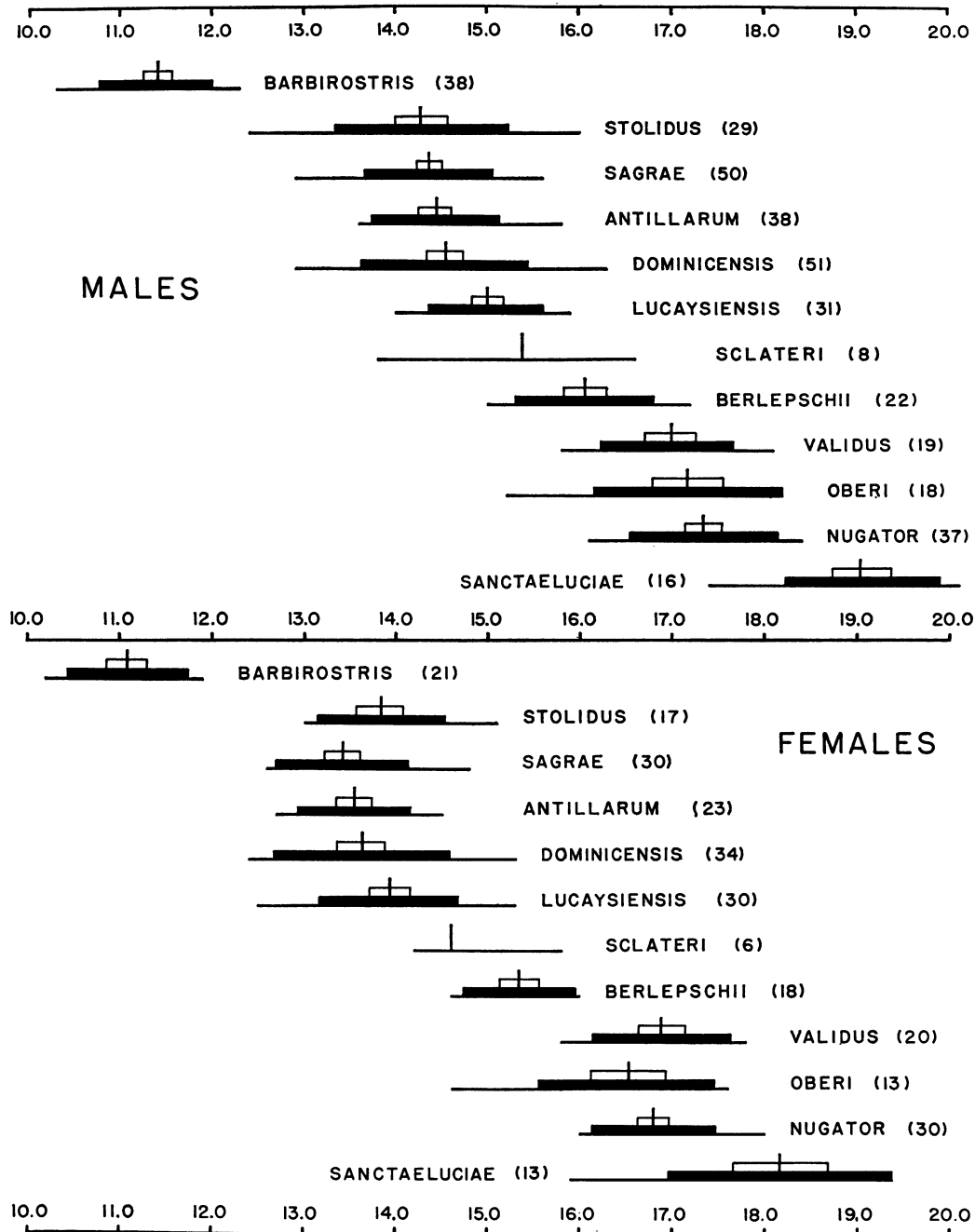


FIG. 3. Population-range diagram of the length of the bill (from the nostril), measured in millimeters, of *Myiarchus* flycatchers of the West Indies. Sample size in parentheses. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation.

having whistled notes in their daytime repertoires, invariably include these whistled notes within their "dawn songs" as well. Evidence is gradually accumulating that suggests that "dawn songs" in this genus have been notably conservative and more resistant to modification with time than other portions of the vocal repertoire. If such is the case, then we might acknowledge that *barbirostris* may well have had whistled notes in its daytime repertoire at one time, but subsequently lost them except for those retained within the "dawn song" assemblage.

The presence or absence of this diagnostic whistled note, perhaps in conjunction with more subtle differences in other vocal patterns, apparently provides a sufficient basis for *barbirostris* and mainland *M. tuberculifer* to discriminate between their respective repertoires. A total of 11 playback experiments were conducted in Jamaica, involving three different territorial males. No nests were found in these territories, though one of the pairs was inspecting holes in coconut palms. The plastic models were not used in this series of experiments because of the possibility that the comparatively large models might inhibit the response of the diminutive *barbirostris*.

Descriptive notes taken in the field of a series of five experiments with one of these males illustrate this discriminatory capability.

EXPERIMENT 103: April 30, 1965, Good Hope, pair number 1; reproductive status unknown. Tapes used, *barbirostris* versus *tuberculifer*; birds calling sporadically in general area at start of experiment. Start at 6:17 A.M. By 6:19 both birds were within 8 feet of *barbirostris* speaker. One criss-crossed within 1 foot of speaker, 6:20, in study at 2 feet from speaker. Very vocal. Intense criss-crossing, all within 10 feet, and mostly within 5 feet of *barbirostris* speaker. Cable switch at 6:24. Both birds reoriented to new *barbirostris* speaker, within 10 feet, by 6:25. Intense criss-crossing, study within 2 feet of speaker. Very vocal. One went to mid-point at 6:28, but returned within 30 seconds. The more active bird stayed within 1 to 4 feet of speaker throughout second half of experiment. Experiment ended at 6:31.

EXPERIMENT 104: Same conditions as in experiment 103. Tapes used, *barbirostris* versus *scelateri* (but location of *barbirostris* speaker reversed from

position at end of experiment 103); both birds in general region, but outside experimental area. Start at 6:34 A.M. Within 1 minute, both birds were within 10 feet of new *barbirostris* speaker. One moved into study at 4 feet, then intense criss-crossing. Other working in wider radius (6–30 feet). Both very vocal. Cable switch at 6:41. Both birds reoriented at once to new *barbirostris* speaker. Same type of intense, vocal response at new location. 6:46, male moved back to 30 feet from speaker (first prolonged absence from near vicinity of *barbirostris* speaker). Calling loudly from this perch at end of experiment at 6:48.

EXPERIMENT 105: Same conditions as in experiment 103. Tapes used, *barbirostris* versus *antillarum* (but *barbirostris* position reversed from that at end of experiment 104); both birds within old *barbirostris* area at start of experiment. Start at 6:51 A.M. Both had reoriented to new *barbirostris* speaker within 1.5 minutes; giving intense vocal response. Criss-crossing. Cable switch at 6:58. Both reoriented at once to new *barbirostris* speaker and continued intense response. 7:01, male calling from study within 8 feet of speaker. Criss-crossing and study until end of experiment at 7:05.

EXPERIMENT 106: Same conditions as in experiment 103. Tapes used, *tuberculifer* versus *validus* [to test stimulus value of *tuberculifer* in absence of *barbirostris* tape]; birds in general area, but exact location unknown. Start at 7:09 A.M. At 7:11, one bird showed within 12 feet of *tuberculifer* speaker, at first calling, but then subsiding into a silent study at 10 feet at 7:12. A *validus* heard from midpoint, but not seen. The single *barbirostris* flew back to perch 30 feet from *tuberculifer* speaker at 7:13. Back to 8 feet from *tuberculifer* speaker at 7:15, but silent. Cable switch at 7:16. The single *barbirostris* moved back to 40 feet and did not reorient to new *tuberculifer* speaker. The *validus* continued to call well from mid-point, but no approach. Both *barbirostris* can be seen feeding at about 40 feet from new *validus* speaker [old *tuberculifer* speaker]. No response to new *tuberculifer* location. End of experiment at 7:23.

EXPERIMENT 107: Same conditions as in experiment 106. Tapes used, *barbirostris* versus *stolidus* (but *barbirostris* speaker situated where *tuberculifer* failed to stimulate them in last experiment); birds silent, location unknown at start of experiment. Start at 7:29 A.M. Within 1 minute, one bird showed at edge of *barbirostris* area. Perched 8 feet from *barbirostris* speaker within 1.5 minutes. In another minute, both birds were within a radius of 10 feet of *barbirostris* speaker, very vocal. 7:33, a pair of *stolidus* showed within 10 feet of *stolidus* speaker. Pair of *barbirostris* at 8 feet and 10 feet of *barbirostris* speaker. Cable

TABLE 4
BILL WIDTH (IN MILLIMETERS) IN SAMPLES OF WEST INDIAN *Myiarchus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>lucaysiensis</i> (Bahamas)					
Males	31	6.8-8.0	7.36±0.05	0.30	4.08
Females	30	6.9-7.9	7.33±0.05	0.28	3.82
<i>sagrae</i> (Cuba, Grand Cayman)					
Males	52	6.5-7.5	7.08±0.03	0.25	3.53
Females	31	6.6-7.9	7.15±0.05	0.27	3.78
<i>stolidus</i> (Jamaica)					
Males	28	6.6-7.2	6.86±0.04	0.22	3.21
Females	19	6.5-7.2	6.94±0.05	0.22	3.17
<i>dominicensis</i> (Hispaniola)					
Males	53	6.1-7.5	6.85±0.05	0.34	4.96
Females	33	6.1-7.5	6.82±0.06	0.33	4.84
<i>antillarum</i> (Puerto Rico)					
Males	38	6.5-7.7	6.99±0.04	0.24	3.43
Females	24	6.5-7.5	6.90±0.05	0.25	3.62
<i>berlepschii</i> (St. Kitts, Nevis, Barbuda)					
Males	24	7.0-8.3	7.85±0.06	0.30	3.82
Females	18	7.4-8.3	7.86±0.06	0.26	3.31
<i>oberi</i> (Dominica and Guadeloupe)					
Males	19	8.1-9.1	8.58±0.08	0.33	3.85
Females	13	8.0-9.1	8.48±0.10	0.37	4.36
<i>sclateri</i> (Martinique)					
Males	8	7.4-7.8	7.61		
Females	6	7.2-7.7	7.53		
<i>sanctaeluciae</i> (St. Lucia)					
Males	16	8.3-9.6	9.09±0.08	0.30	3.30
Females	13	8.5-10.0	9.15±0.11	0.38	4.15
<i>validus</i> (Jamaica)					
Males	21	8.2-9.1	8.54±0.05	0.23	2.69
Females	19	8.1-9.1	8.72±0.06	0.28	3.21
<i>barbirostris</i> (Jamaica)					
Males	38	6.4-7.7	7.02±0.05	0.30	4.27
Females	21	6.6-7.3	6.98±0.04	0.19	2.72
<i>nugator</i> (Grenada, Grenadines, and St. Vincent)					
Males	38	8.1-9.3	8.69±0.05	0.33	3.80
Females	30	8.1-9.6	8.69±0.06	0.31	3.57

switch at 7:36. Both *barbirostris* reoriented to new *barbirostris* area, while *stolidus* moved to mid-point. Both *barbirostris* within 8 feet of *barbirostris* speaker at 7:39, calling well. *Stolidus* left experimental area. Both *barbirostris* dropped back to 30 feet of *barbirostris* speaker, calling well. End of experiment at 7:43.

When in Yucatán in 1963, I conducted similar experiments with territorial males of *M. tuberculifer platyrhynchus*, and found that they would not respond to playback of

barbirostris repertoire. Therefore, although we must admit that they are closely allied, the evidence suggests that *barbirostris* should be considered specifically distinct from *M. tuberculifer*.

***Myiarchus stolidus* (Gosse)**

***Myiarchus stolidus stolidus* (Gosse)**

Myiobius stolidus Gosse, 1847, p. 168.

Myiarchus stolidus stolidus: HELLMAYR, 1927, p. 170 (synonymy). BOND, 1956, p. 107.

RANGE AND SPECIMENS EXAMINED: Jamaica (48).

This last of three Jamaican species of *Myiarchus*, *stolidus*, can be separated readily from its sympatric congeners (*barbirostris* and *validus*) by either mensural characters or by rectrix coloration (see key, p. 334, and text figs. 1-3). Morphologically, *stolidus* is closest to *dominicensis* of Hispaniola from which it is nearly but not completely separable by lacking a prominent, well-defined cinnamon stripe on the sixth rectrix. The relationship of *stolidus* to *M. yucatanensis* of the Yucatán Peninsula of Mexico has been considered elsewhere (Lanyon, 1965). I concluded that the Yucatán form was specifically distinct and not necessarily more closely related to *stolidus* than to other congeners. The mouth lining of *stolidus* is pale orange like that of *dominicensis*, and hence somewhat lighter in color than that of *yucatanensis*, but richer than the pale yellow lining of *sagrae*, *lucaysiensis*, *antillarum*, and the races of *M. oberi* in the Lesser Antilles.

The vocal repertoire of *stolidus*, illustrated in plate 27, shows no greater deviation from that of *dominicensis* (pl. 28) of Hispaniola than one would expect to find between two races of a continental *Myiarchus*. It is of interest that the "dawn song" of *stolidus* (pl. 27, figs. 1 and 4) shows some similarity to that of *sagrae* (pl. 23, figs. 1 and 3) and *lucaysiensis* (pl. 23, figs. 1 and 3), in that the middle and terminal components are essentially identical. Only with respect to the introductory component, which is a whistled note in the case of *stolidus*, is there a significant difference. As indicated above, *lucaysiensis* and *sagrae* do not have whistled notes in their daytime repertoires, and the introductory component in their "dawn songs" is a modified "huit" note instead. A whistled note, fairly prolonged and ascending in frequency, is a diagnostic feature of the daytime repertoire of *stolidus* (pl. 27, fig. 6). This is the vocal pattern that Bond (1961a, p. 154) referred to as "a shrill oo-ee" and that is responsible for the local name "Louis." A two-syllabled "wick-up" note (pl. 27, fig. 2), a shrill, rolling "pee-r-r-r" note (pl. 27, fig. 3), a rasping note (pl. 27, fig. 7), and a series of emphatic "huit, huit" notes (pl. 27, fig. 5)

constitute the remaining components of the daytime repertoire of *stolidus*.

A total of 14 experiments were conducted in Jamaica, involving four different territorial males. No nests were found, and I was unable to determine the breeding status of these experimental birds. All four of these males were able to discriminate between their own vocal repertoire and those of *antillarum*, *lucaysiensis*, and other congeners. No tape of *dominicensis* was available at the time of these particular experiments. Subsequently, tapes of *stolidus* were presented to territorial males of *dominicensis* in Haiti (see p. 350).

Descriptive notes taken in the field of six experiments with two *stolidus* males follow:

EXPERIMENT 124: May 5, 1965, Good Hope, pair number 3. Tapes used, *lucaysiensis* versus *antillarum*; birds calling from general area at start of experiment. Start at 6:13 A.M. One bird showed in coconut palm over *antillarum* speaker (40 feet up), silent, within 1 minute. Remained there, silent, until 6:16, then flew to another palm 200 feet away and outside experimental area. Calling sporadically from outside area for rest of experiment. End of experiment at 6:20.

EXPERIMENT 125: Same conditions as in experiment 124. Tapes used, *stolidus* versus *nugator* [to test stimulus value of *stolidus* tape, following poor response to *antillarum* and *lucaysiensis* in previous experiment]; birds silent, exact location unknown at start of experiment. Start at 6:22 A.M. One showed at once, perched within 4 feet of *stolidus* model, calling well. Moved to 6 feet, giving rasping notes. 6:24, criss-crossing. Moved to 18 inches of mount at 6:25, calling well. 6:26, flew to coconut palm outside experimental area, calling, then dropped back into *stolidus* area again at 6:28. Perched 10 feet from mount. Cable switch at 6:29, when male was 6 feet from the old *stolidus* model. Within 1 minute, male had reoriented to new *stolidus* area, perched in palm directly above speaker, calling well. Down to ground level at 6:31, perched 20 feet from new *stolidus* model. Criss-crossed *stolidus* area at 6:32. Female showed at this point, joined male in flying excitedly between palms nearest *stolidus* model. 6:35, male perched on fence post 12 feet from *stolidus* model, giving rasping notes. Criss-crossed model just before experiment ended at 6:36.

EXPERIMENT 126: Same conditions as in experiment 125. Tapes used, *stolidus* versus *lucaysiensis* (but location of *stolidus* area reversed from that at end of experiment 125); birds calling outside of experimental area at start of experiment. Start at

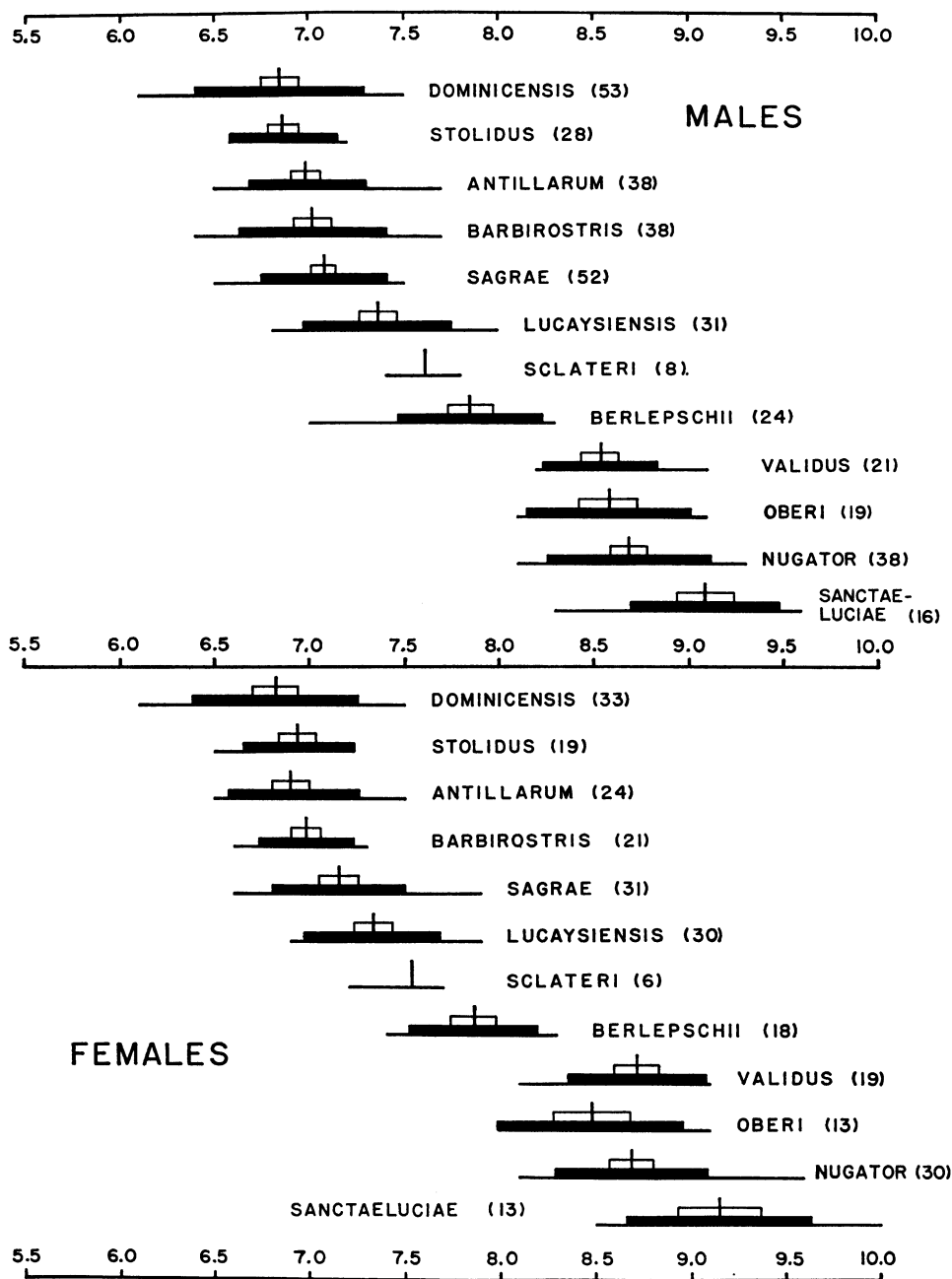


FIG. 4. Population-range diagram of the width of the bill (at the nostril), measured in millimeters, of *Myiarchus* flycatchers of the West Indies. Sample size in parentheses. Horizontal lines represent range; means are indicated by vertical lines; open rectangles indicate twice the standard error of the mean; solid rectangles indicate 1.3 times the standard deviation.

6:45 A.M. Both came over at once to palm at edge of experimental area, calling. Flying back and forth in palms nearest new *stolidus* area. Criss-crossing over *stolidus* model, about 25 feet overhead. 6:48, one swooped low over *stolidus* model. Cable switch at 6:52. At 6:53, male flew to palm outside experimental area, giving rasping notes. 6:54, male moved to ground level, perching in bushes 40 feet from new *stolidus* speaker. Moving closer to model. 6:56, male perched 20 feet from model. A pass within 1 inch of *stolidus* model; bill-snapping during this pass. Criss-crossing at 6:57, calling loudly. Perched 5 feet from *stolidus* model at 6:58. End of experiment at 6:59.

EXPERIMENT 127: Same conditions as in experiment 125. Tapes used, *stolidus* versus *antillarum* (but location of *stolidus* speaker reversed from end of last experiment); birds silent, location unknown at start of experiment. Start at 9:15 A.M. At 9:18, one showed in coconut palm directly above *stolidus* speaker, 40 feet up, calling, looking down at speaker. Still there at cable switch at 9:22. Male flew to a palm over the new *stolidus* speaker within 1 minute. 9:28, male dropped to ground level, perched in bushes 15 feet from *stolidus* model. Remained there, in study, until end of experiment at 9:29.

EXPERIMENT 128: May 5, 1965, Good Hope, pair number 4. Tapes used, *stolidus* versus *antillarum*; birds calling from general area just prior to start of experiment. Start at 10:08 A.M. One showed in *stolidus* area within 1 minute; perched 8 feet from *stolidus* model, calling well. Criss-crossing at 10:10. Moved into a study at 5 feet at 10:11. Excited, moving within radius of 6 feet of model, calling well. 10:12, a pass over the model, calling loudly. 10:14, another pass. Still close to model at cable switch at 10:15. Male reoriented to new *stolidus* speaker at once. Perched 6 feet from new *stolidus* model at 10:17. A pass. 10:19, male left experimental area, joined female outside of area and remained there (200 feet away) until end of experiment at 10:22. Within 30 seconds after cessation of tape, male flew back into experimental area and perched 3 feet from the *stolidus* model.

EXPERIMENT 129: Same conditions as in experiment 128. Tapes used, *stolidus* versus *lucaysiensis* (but reversed position of *stolidus* speaker); male still perched within 3 feet of what was the *stolidus* model at end of experiment 128. Start at 10:26 A.M. Within 1 minute, male flew over to hedgerow outside experimental area, then flew directly to new *stolidus* model, perched 5 feet away. 10:30, perched 4 feet from model, calling well. 10:31, male dove at and struck the *stolidus* model. Three more attacks. Cable switch at 10:33. Just after the switch, both birds were in the new *lucaysiensis*

TABLE 5

BILL LENGTH (IN MILLIMETERS) IN *Myiarchus barbirostris* AND *M. tuberculifer platyrhynchus*

Sample	N	Range	Mean
<i>barbirostris</i>			
Males	38	10.3–12.3	11.41
Females	21	10.2–11.9	11.08
<i>platyrhynchus</i>			
Males	31	12.0–14.6	13.10
Females	9	12.1–12.8	12.48

area. By 10:34, male had reoriented to 40 feet from new *stolidus* model. Made a pass at model; perched 3 feet away. Criss-crossing; another pass. 10:38, more criss-crossing and passing. Female joined him at 10:39, 40 feet from *stolidus* model; male still making passes at model until end of experiment at 10:40. Two minutes after cessation of tape, the male struck the *stolidus* model, spinning it around on the perch.

Myiarchus stolidus dominicensis (Bryant)

Tyrannula stolidus (var. *dominicensis*) BRYANT, 1867b, p. 90.

Myiarchus dominicensis: CORY, 1885, p. 79. RIDGWAY, 1907, p. 634 (synonymy).

Myiarchus stolidus dominicensis: HELLMAYR, 1927, p. 169 (synonymy). BOND, 1956, p. 108.

RANGE AND SPECIMENS EXAMINED: Hispaniola: Haiti (48) and the Dominican Republic (40).

This Hispaniolan *Myiarchus* is closest to *stolidus* of Jamiaca with respect to morphological characters (see text figs. 1–4 and the key on p. 335), but is almost invariably distinguishable from that representative form by the presence of a prominent, well-defined cinnamon stripe on the sixth rectrix. Both forms have a pale orange mouth lining which is a shade brighter or richer than the pale yellow lining shared by *antillarum*, *sagrae*, *lucaysiensis*, and the races of *M. oberi* in the Lesser Antilles. From a populational viewpoint, Ridgway's statement (1907, p. 634) that *dominicensis* is "slightly larger [than *stolidus*]" is erroneous (see text figs. 1–4).

As indicated above, *dominicensis* and *stolidus* share the same vocal repertoire (pls. 27 and 28), thus confirming the close relationship suggested by morphology. Similarity

between certain vocal patterns of *dominicensis* and those of the Puerto Rican *antillarum* (pl. 29) is discussed in some detail in the account of the latter form.

When in Haiti in 1966 I had an opportunity to test the discriminatory ability of two territorial males of *dominicensis* to the playback of *stolidus* vocal patterns and also to the repertoires of other congeners. These males were unable to differentiate between their own repertoire and that of *stolidus*, i.e. their responses were not consistently stronger to one than to the other. When presented with a choice between their own repertoire and that of *antillarum* of Puerto Rico, they responded to their own repertoire more strongly than to repertoire of *antillarum* but with some inconsistencies. They did not react positively to any other *Myiarchus* repertoire. The following field notes illustrate these points:

EXPERIMENT 134: May 13, 1966, Haiti, pair number 1; reproductive status unknown. Tapes used, *dominicensis* versus *antillarum*; birds silent, location unknown at start of experiment. Start at 5:30 A.M. One bird first appeared at *dominicensis* speaker within 30 seconds. By 5:32, two birds were in experimental area, had moved briefly to mid-point, then back into *dominicensis* area. 5:33 one moved back to mid-point, then rejoined second bird in *dominicensis* area. 5:34, both birds at *dominicensis* model, criss-crossing. One 6 feet from model. Just before switch, at 5:35, both birds had moved to within 4 feet of *antillarum* model, and both were at that point when cables were switched. Both remained at new *dominicensis* model throughout remaining 5 minutes of playback, calling well; one in good study within 3 feet of *dominicensis* model at 5:39. At end of experiment at 5:40, both birds were still within 20 feet of *dominicensis* model.

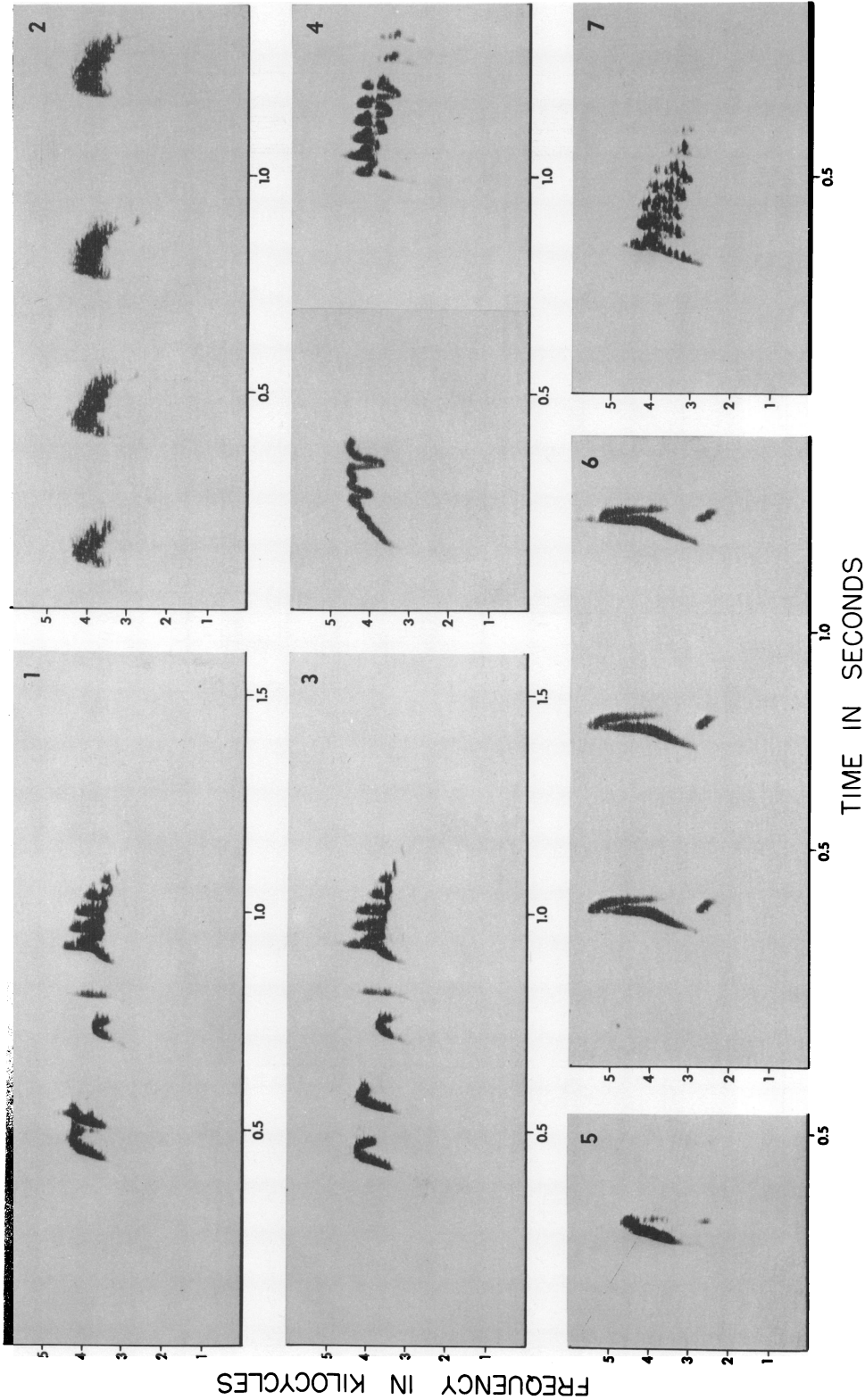
EXPERIMENT 135: Same conditions as in experiment 134. Tapes used, *dominicensis* versus *stolidus* (but location of *dominicensis* speaker reversed from that at end of experiment 134); both birds at former *dominicensis* area, now occupied by *stolidus* speaker, at beginning of this experiment. Start at 5:42 A.M. Both birds in *stolidus* area. By 5:44, one had moved to mid-point, then continued on to *dominicensis* area. 5:45, calling well within 3 feet of *dominicensis* model. Then both birds moved back to *stolidus* area, calling well. 5:46, one made a pass over *stolidus* model. Both moved to mid-point, then back to *stolidus* area at time of cable switch, at 5:47. One remained 2 feet

from new *dominicensis* speaker, while other one moved to mid-point. 5:49, one bird passed over *stolidus* model, while the second bird made a pass at the *dominicensis* model. At 5:50, one bird at each experimental area. 5:51, both birds now at *dominicensis* area, remained there until end of experiment.

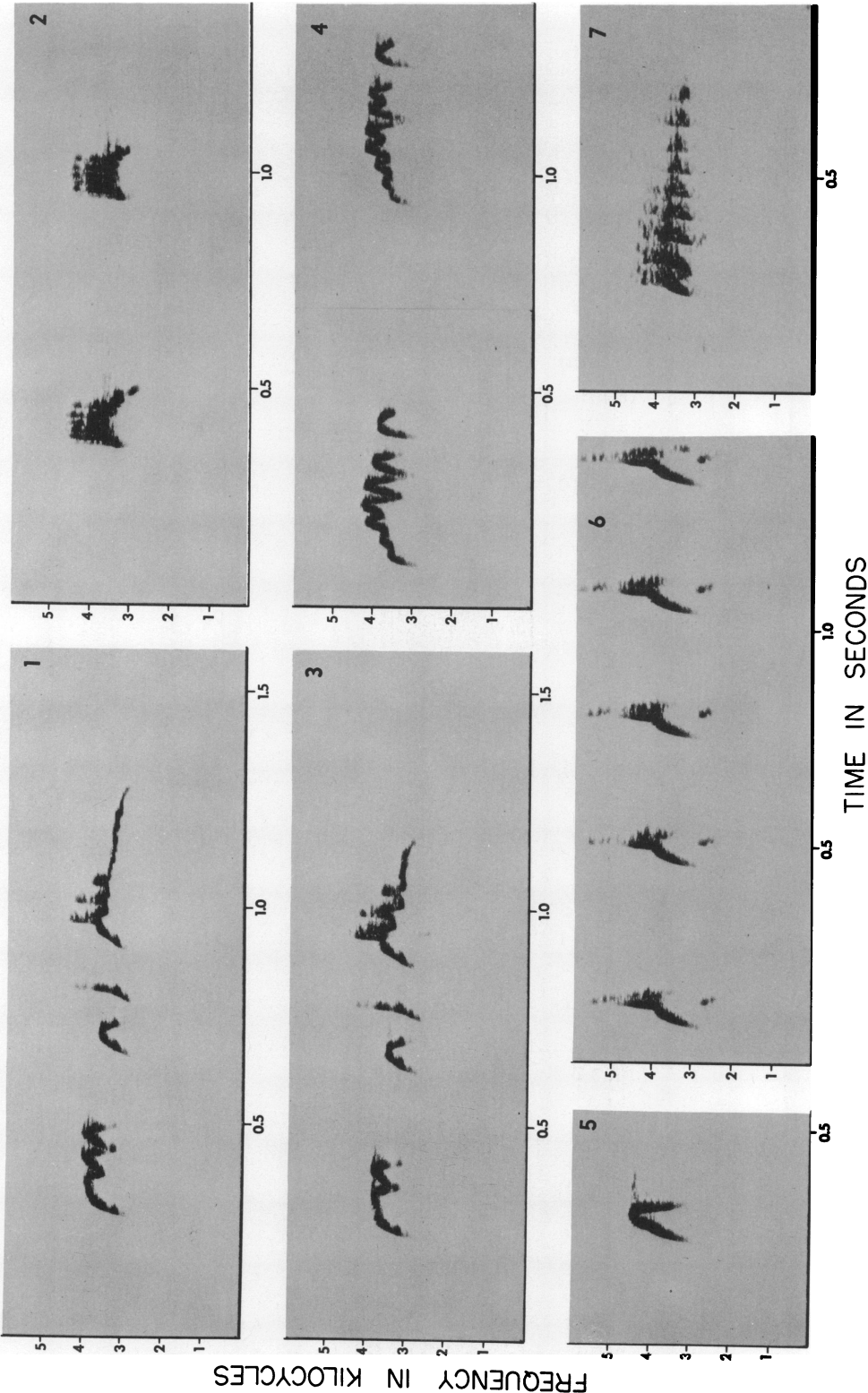
EXPERIMENT 136: Same conditions as in experiment 134. Tapes used, *stolidus* versus *sclateri*; location of birds unknown at start of experiment. Start at 6:00 A.M. One bird appeared within 30 seconds, perched within 2 feet of *stolidus* model. By 6:02, two birds were within 10 feet of *stolidus* model. Both in study at 10 feet from *stolidus* model at 6:03. One moved to mid-point at 6:04, but both back at *stolidus* model at time of cable switch at 6:05. Within 30 seconds, both birds reoriented to new *stolidus* location. Still within 15 feet of *stolidus* model at 6:07. 6:08, one left experimental area, the other 50 feet from *stolidus* model. Both out of experimental area at end of experiment at 6:10.

EXPERIMENT 137: Same conditions as in experiment 134. Tapes used, *lucaysiensis* versus *dominicensis*; birds out of experimental area at start of experiment. Start at 6:12 A.M. Both birds showed at once in *dominicensis* area, within 10 feet of model. At 6:14, one moved to mid-point, feeding there, but then back to *dominicensis* area, calling well. 6:16, one 15 feet from *dominicensis* model; made a pass 2 feet from this model just before cable switch at 6:17. Within 15 seconds, both birds had reoriented to new *dominicensis* speaker. Except for two brief visits back into *lucaysiensis* area, both birds remained within *dominicensis* area for rest of experiment, approaching to within 6 feet of model on frequent occasions.

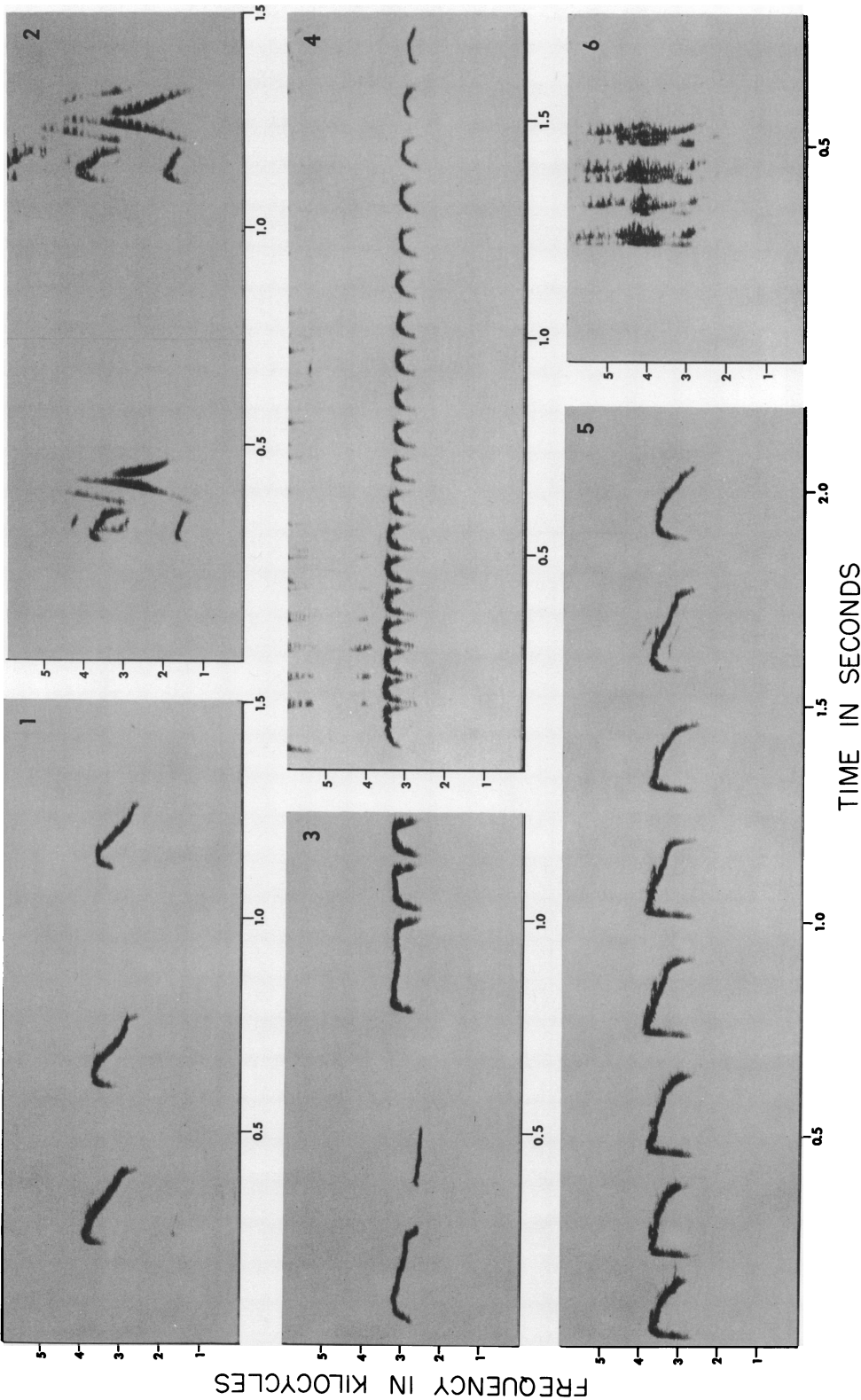
EXPERIMENT 139: May 13, 1966, Haiti, pair number 2; reproductive status unknown. Tapes used, *dominicensis* versus *stolidus*; location of birds unknown at start of experiment. Start at 8:30 A.M. Both birds oriented at once to *stolidus* speaker, calling well within 15 feet of the model. At 8:32, both had moved to mid-point, then briefly over to *dominicensis* area, but back to *stolidus* area by 8:33. At 8:34, both calling well within 15 feet of *stolidus* model. Both in *stolidus* area at time of cable switch at 8:35. Both birds reoriented to new *stolidus* speaker after cable switch, then moved to mid-point, and back to *dominicensis* area. 8:37, still calling well within 30 feet of *dominicensis* model. 8:38, both moved at once to *stolidus* area, and perched 10 feet from *stolidus* model. Back to mid-point, then back into *stolidus* area. 8:39, criss-crossing over *stolidus* area. Back to mid-point, then criss-crossing in *dominicensis* area just before end of experiment at 8:40.



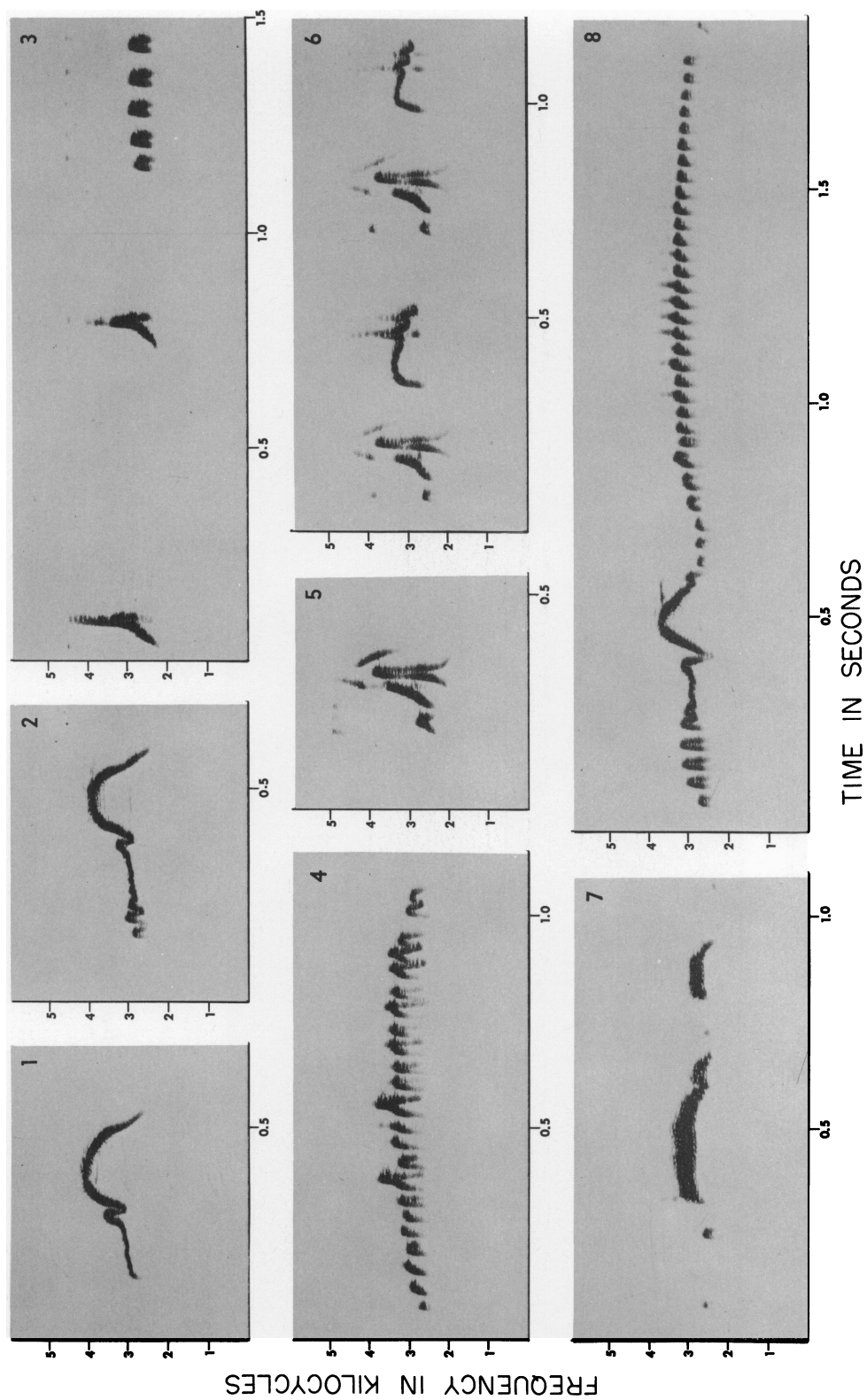
Sound spectrograms of *M. sagrae lucayensis*, recorded on New Providence, Bahamas, in April, 1963, and May, 1965



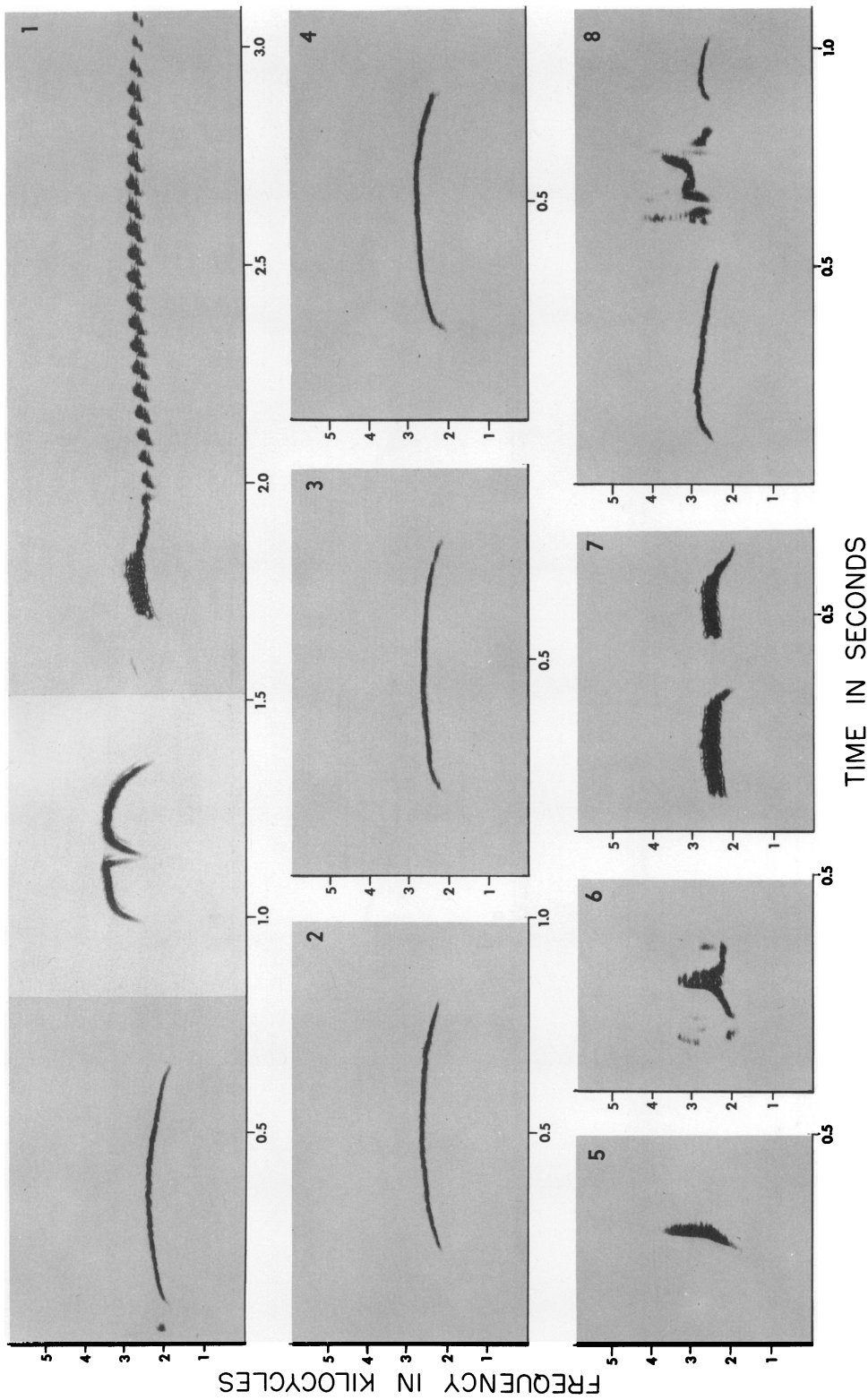
Sound spectrograms of vocalizations of *M. sagrae sagrae*, recorded on Grand Cayman, Cayman Islands, in May, 1966



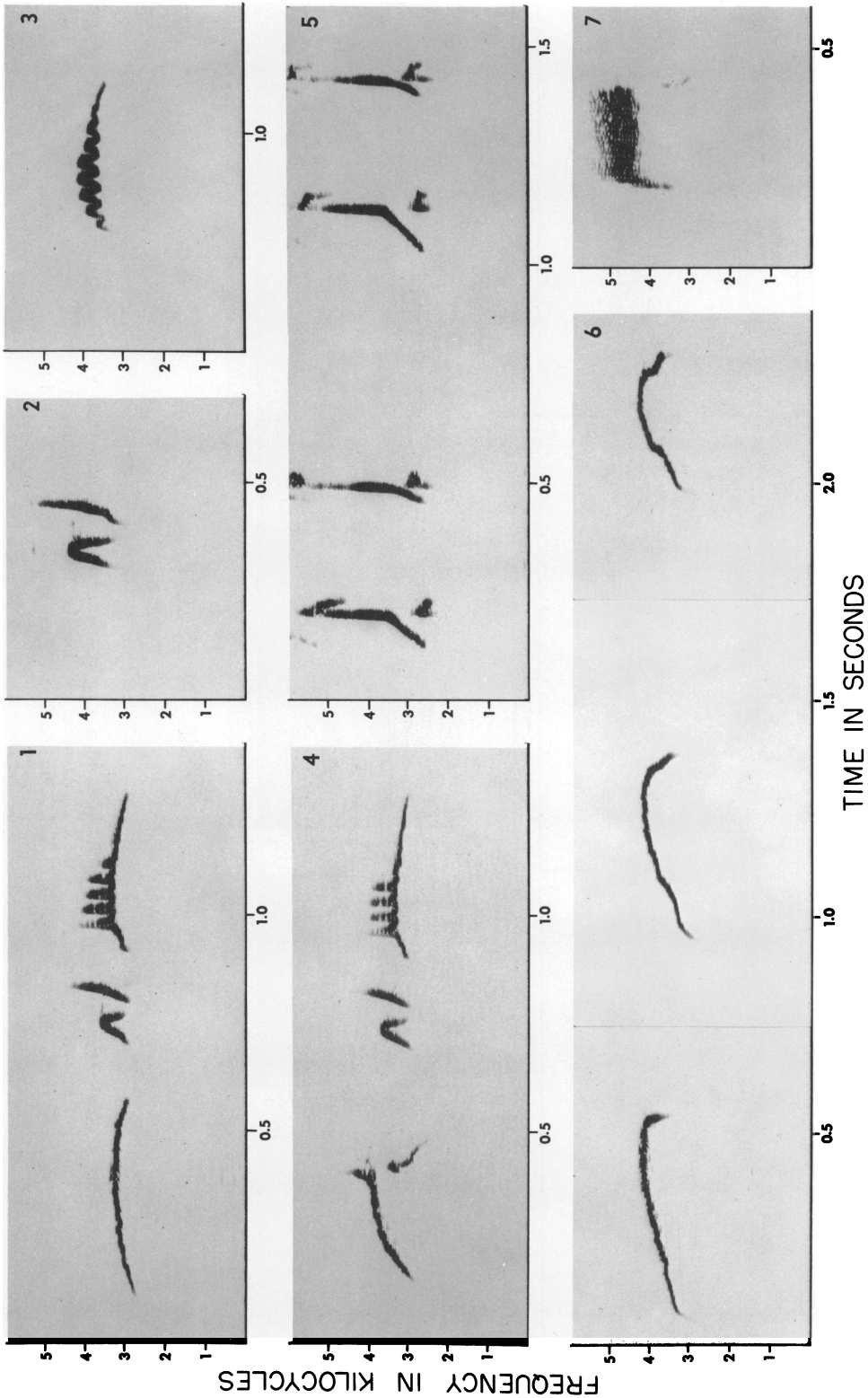
Sound spectrograms of vocalizations of *M. validus*, recorded at Good Hope, Trelawny Parish, Jamaica, in April, 1963



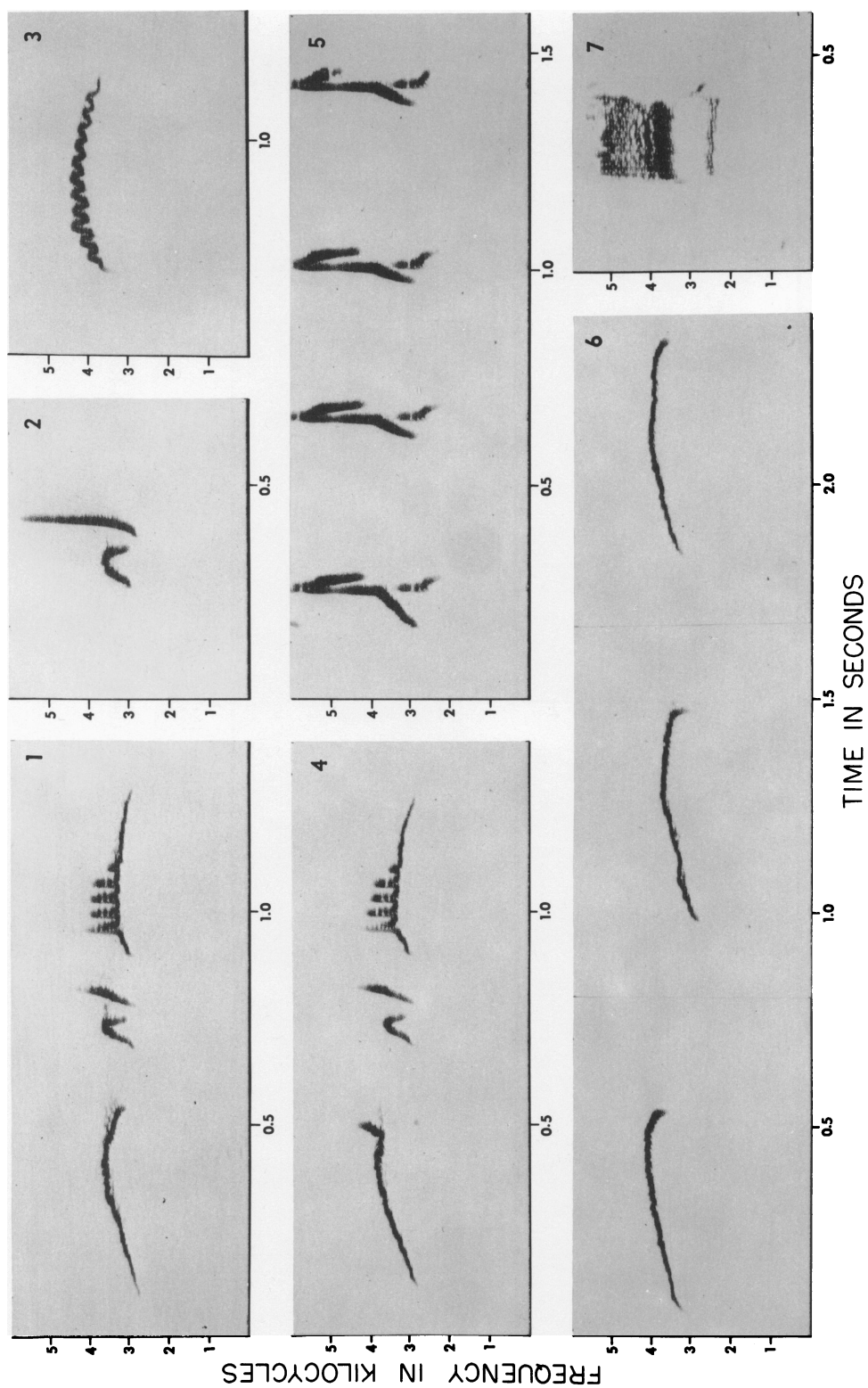
Sound spectrograms of vocalizations of *M. barbivostis*, recorded at Good Hope, Trelawny Parish, Jamaica, in April, 1963



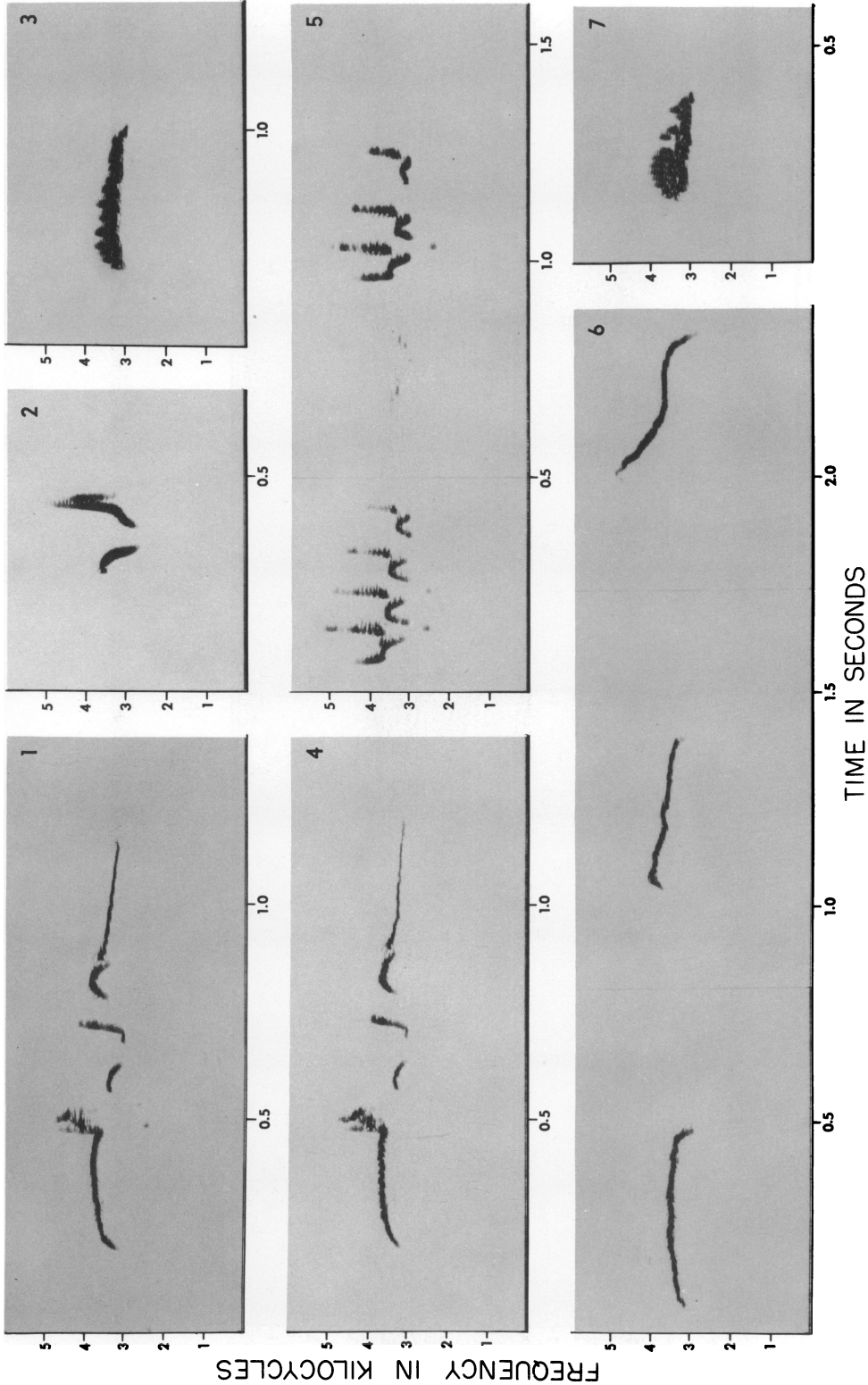
Sound spectrograms of vocalizations of *M. tuberculifer*. 1. "Dawn song" recorded near Chichén Itzá, Yucatán, Mexico, in April, 1963 (*M. t. platyrhynchus*). 2. Portal, Arizona, in June, 1957 (*M. t. olivascens*). 3. Tonalá, Chiapas, Mexico, in May, 1959 (*M. t. laurencei*). 4. La Union, El Salvador, in April, 1959 (*M. t. connectens*). 5-7. Chichén Itzá, Yucatán, Mexico, in April, 1963 (*M. t. platyrhynchus*). 8. Portal, Arizona, in June, 1957 (*M. t. olivascens*)



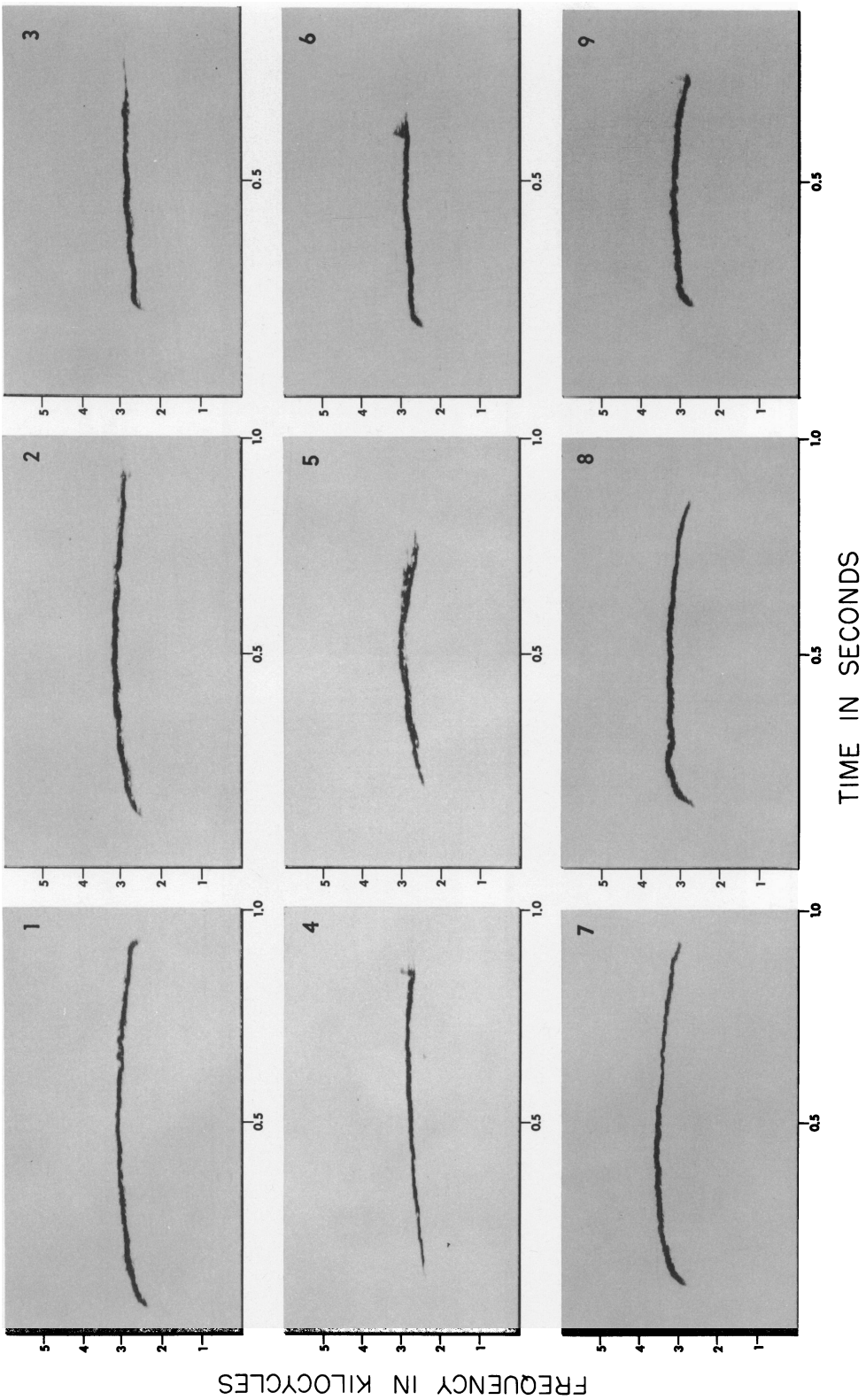
Sound spectrograms of vocalizations of *M. stolidus stolidus*, recorded at Good Hope, Trelawny Parish, Jamaica, in April, 1963, and May, 1965



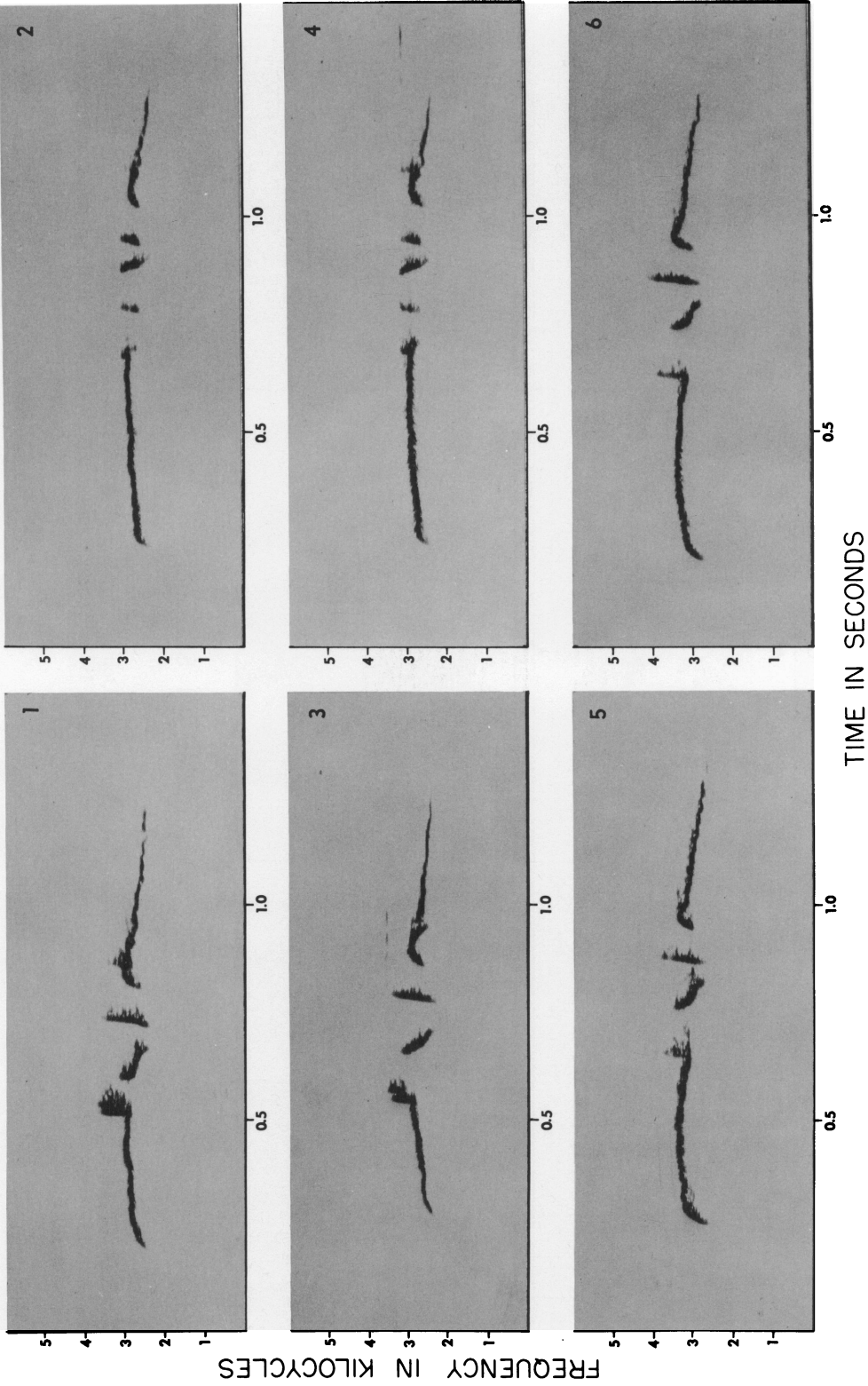
Sound spectrograms of vocalizations of *M. stolidus dominicensis*, recorded near Port-au-Prince, Haiti, in May, 1966



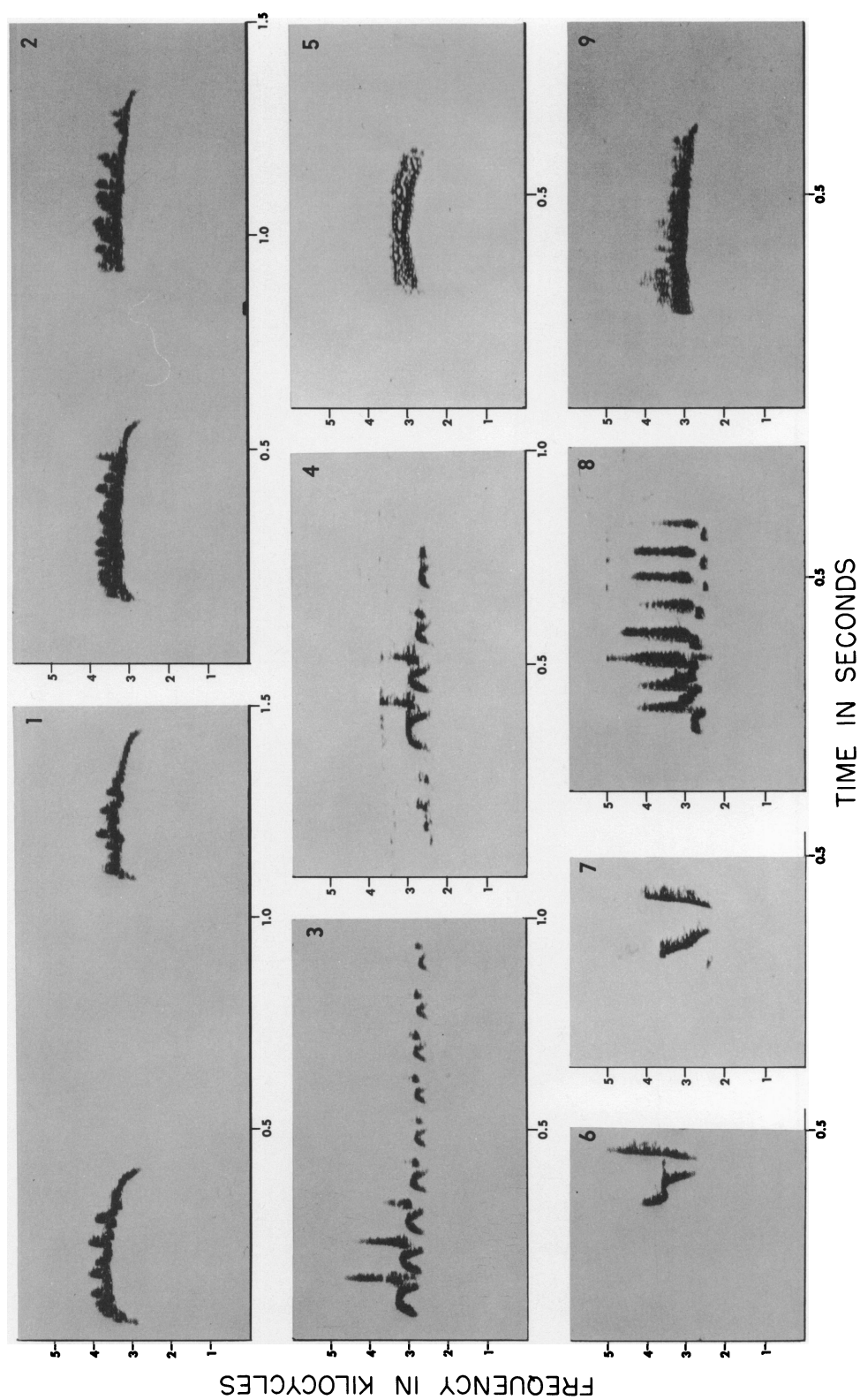
Sound spectrograms of vocalizations of *M. anillarum*, recorded in the Guánica Forest Reserve, Puerto Rico, in April, 1963, and April, 1965



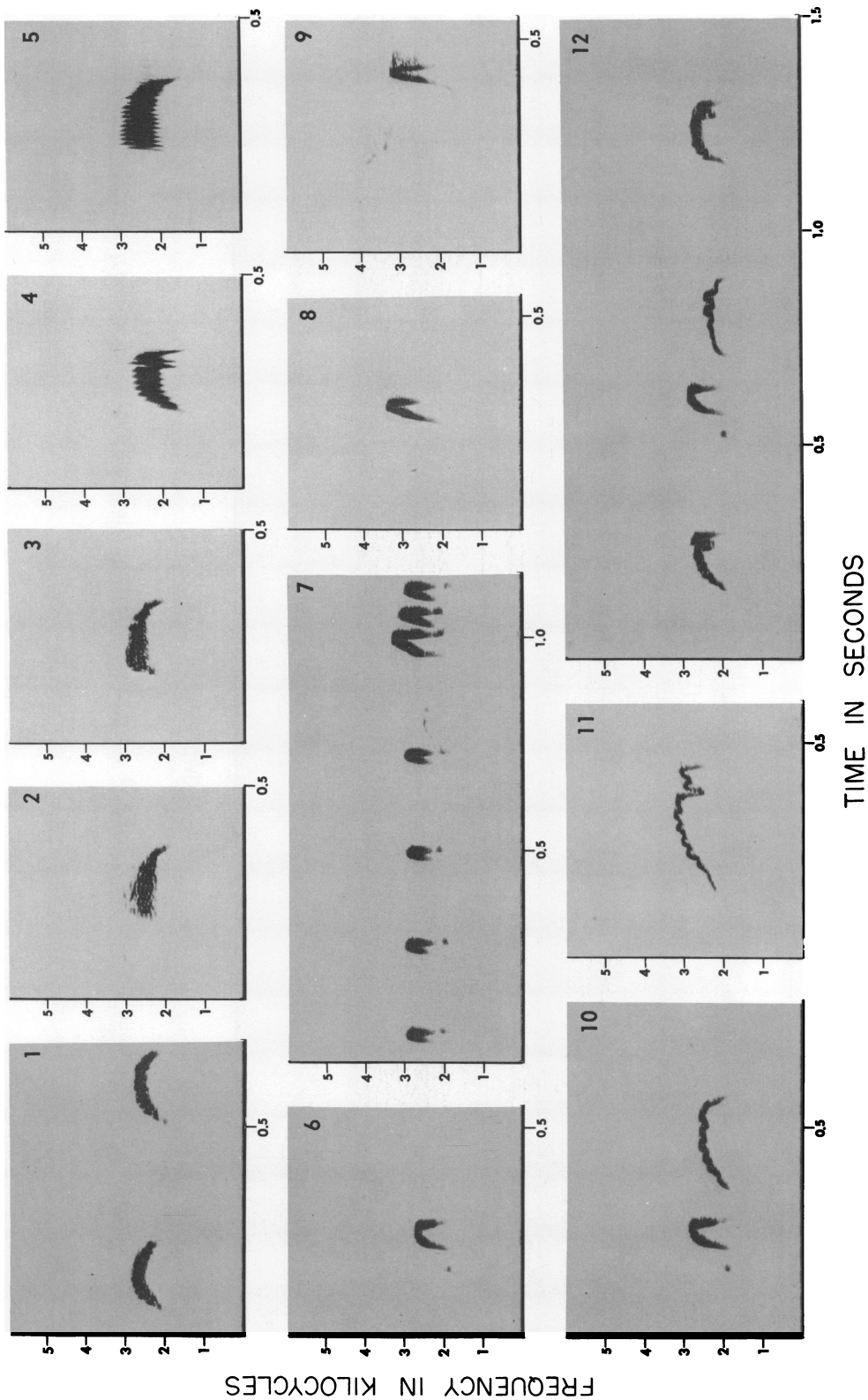
Sound spectrograms of vocalizations of *M. oberi*. 1, 2. Springfield, Dominica, in March, 1963 (*M. o. oberi*). 3, 6. Forestière, St. Lucia, in May, 1966 (*M. o. sanctaeluciae*). 4, 5. Molyneux, St. Kitts, in April, 1965 (*M. o. berlepschii*). 7-9. Trois Ilets, Martinique, in April, 1965 (*M. o. sclateri*)



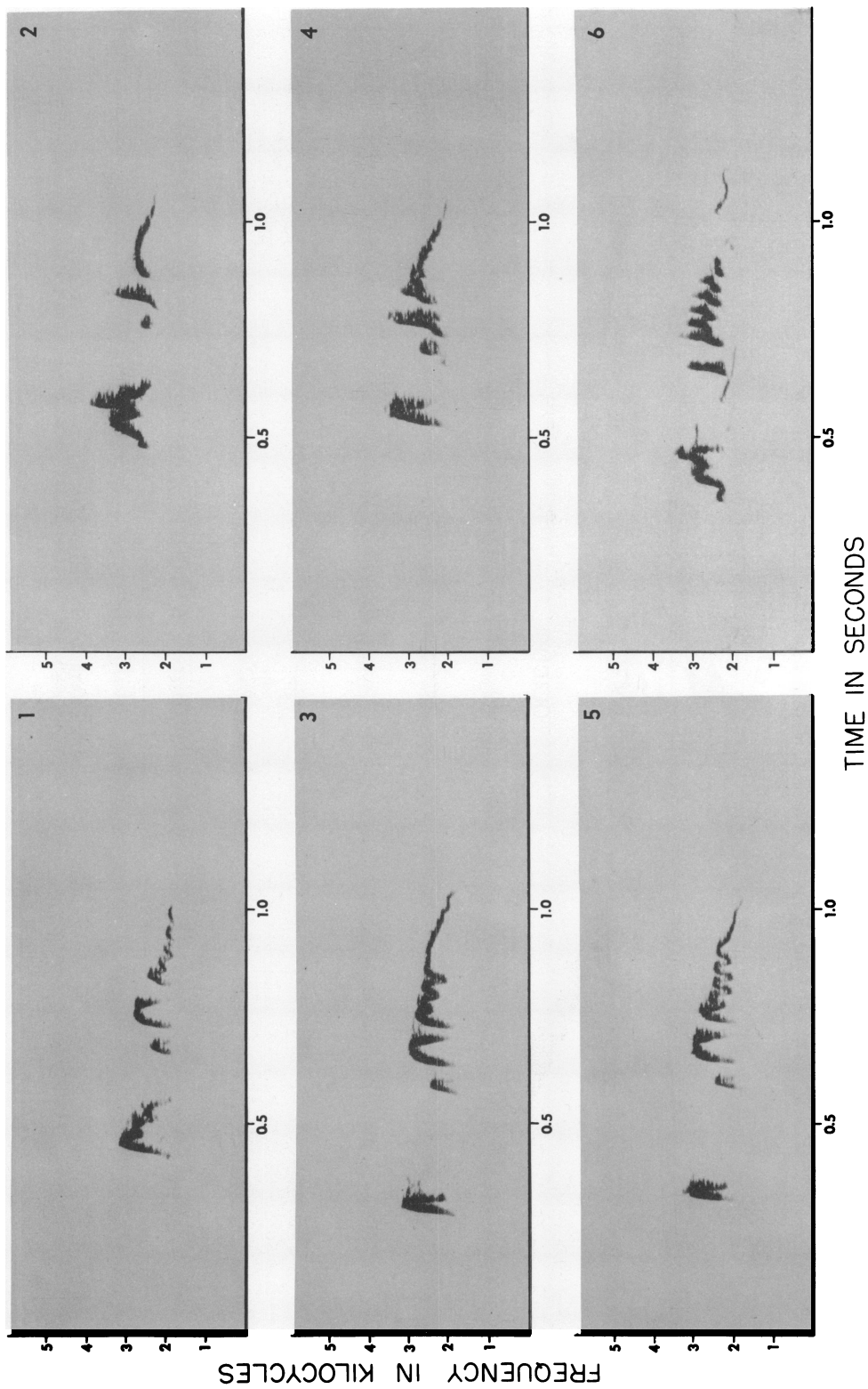
Sound spectrograms of "dawn songs" of *M. o. oberi*. 1. Springfield, Dominica, in March, 1963 (*M. o. oberi*). 2, 4. Forestière, St. Lucia, in May, 1966 (*M. o. sanctaeluciae*). 3. Molyneux, St. Kitts, in April, 1965 (*M. o. berlepschi*). 5, 6. Trois Ilets, Martinique, in April, 1965 (*M. o. sclateri*)



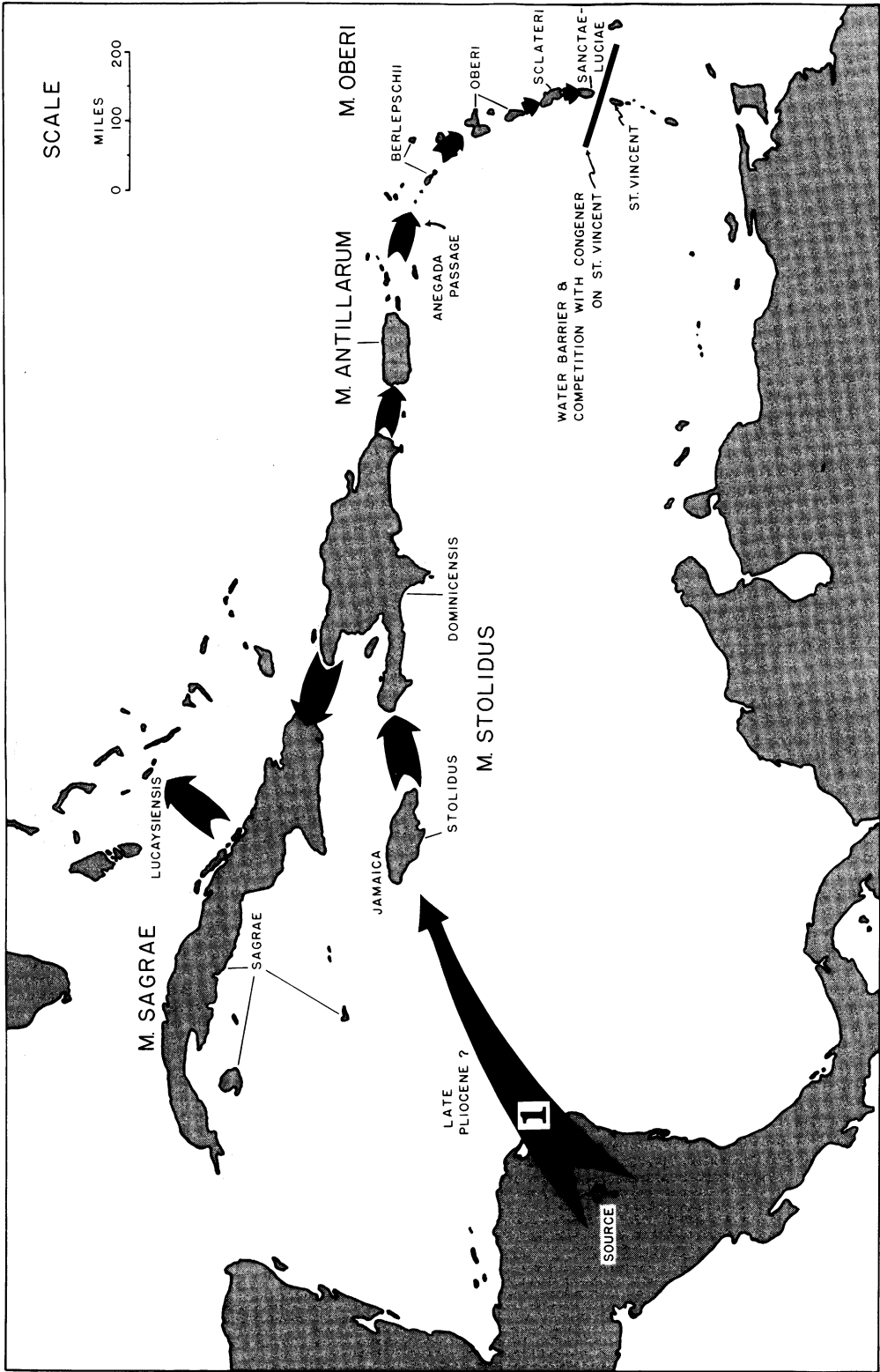
Sound spectrograms of vocalizations of *M. oberi*. 1, 3, 6, 8, 9. Trois Ilets, Martinique, in April, 1965 (*M. o. sclateri*). 2, 4, 5, 7. Molyneux, St. Kitts, in April, 1965 (*M. o. berlepschii*)



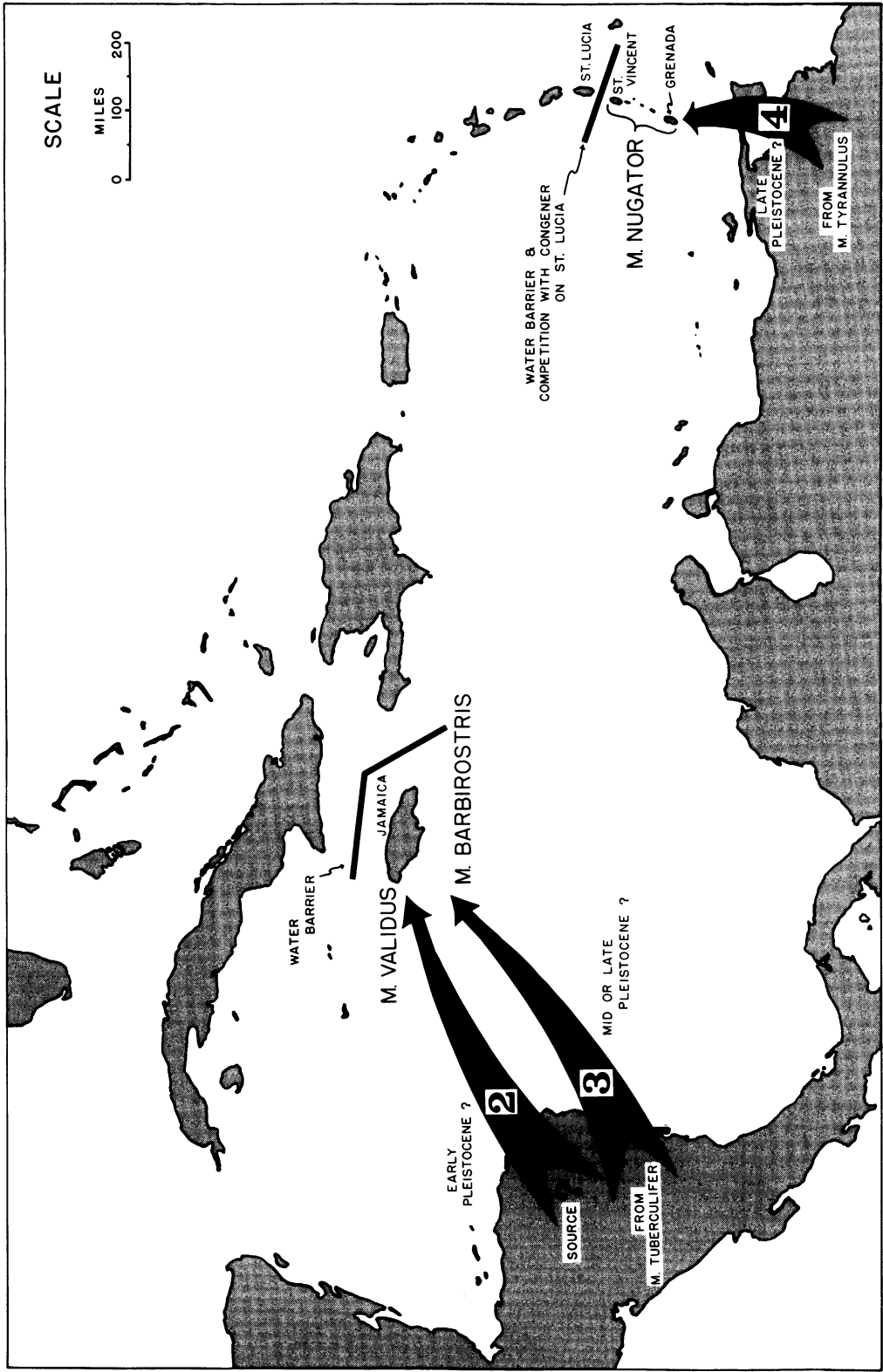
Sound spectrograms of vocalizations of *M. nugar* and of *M. tyrannulus*. 1, 4, 6, 7, 10, 12. Recorded in St. George Parish, Grenada, in April, 1965 (*M. nugar*). 2. Recorded on Monos Island, Trinidad, in March, 1963 (*M. t. tyrannulus*). 3, 5. Recorded near Portal, Arizona, in June, 1959 (*M. t. magister*). 8. Recorded near Liberia, Costa Rica, in April, 1959 (*M. t. brachyurus*). 9. Recorded near Chichén Itzá, Yucatán, Mexico, in May, 1959 (*M. t. cooperi*). 11. Recorded near Barranca, Costa Rica, in April, 1959 (*M. t. brachyurus*).



Sound spectrograms of "dawn songs" of *M. nugar* and of *M. tyrannulus*. 1, 3, 5. Recorded in St. George Parish, Grenada, in April, 1965 (*M. nugar*). 2, 4. Recorded near Barranca, Costa Rica, in April, 1959 (*M. t. brachyurus*). 6. Recorded on Monos Island, Trinidad, in March, 1963 (*M. t. tyrannulus*)



The first of four primary invasions of the West Indies by continental forms of the genus *Myiarchus*, and the subsequent evolution of the super-species *Myiarchus stolidus* from proto-*stolidus* of Jamaica



Three of four primary invasions of the West Indies by continental forms of the genus *Myiarchus*, resulting in the formation of three monotypic and endemic Antillean species

TABLE 6
PREVIOUS AND PROPOSED TAXONOMY OF THE *Myiarchus* FLYCATCHERS OF THE WEST INDIES

Ridgway (1907)	Hellmayr (1927)	Bond (1956), Zimmer (MS) ^a	Present Paper
<i>Hylonax validus</i>	<i>Hylonax validus</i>	<i>M. validus</i>	<i>M. validus</i>
<i>M. barbirostris</i>	<i>M. barbirostris</i>	<i>M. barbirostris</i> ^b	<i>M. [barbirostris]^c barbirostris</i> <i>M. [stolidus] stolidus</i>
<i>M. stolidus</i>	<i>M. stolidus stolidus</i>	<i>M. stolidus stolidus</i>	<i>M. stolidus stolidus</i>
<i>M. dominicensis</i>	<i>M. stolidus dominicensis</i>	<i>M. stolidus dominicensis</i>	<i>M. stolidus dominicensis</i> <i>M. [stolidus] sagrae</i>
<i>M. sagrae sagrae</i>	<i>M. stolidus sagrae</i>	<i>M. stolidus sagrae</i>	<i>M. sagrae sagrae</i>
<i>M. sagrae lucayensis</i>	<i>M. stolidus lucayensis</i>	<i>M. stolidus lucayensis</i>	<i>M. sagrae lucayensis</i>
<i>M. denigratus</i>	Synonymized with <i>sagrae</i>	Synonymized with <i>sagrae</i>	Synonymized with <i>sagrae</i>
<i>M. antillarum</i>	<i>M. stolidus antillarum</i>	<i>M. stolidus antillarum</i>	<i>M. [stolidus] antillarum</i> <i>M. [stolidus] oberi</i>
<i>M. oberi oberi</i>	<i>M. tyrannulus oberi</i>	<i>M. tyrannulus oberi</i>	<i>M. oberi oberi</i>
<i>M. oberi berlepschii</i>	<i>M. tyrannulus berlepschii</i>	<i>M. tyrannulus berlepschii</i>	<i>M. oberi berlepschii</i>
Not yet described	<i>M. tyrannulus sanctaeluciae</i>	<i>M. tyrannulus sanctaeluciae</i>	<i>M. oberi sanctaeluciae</i>
<i>M. sclateri</i>	<i>M. sclateri</i>	<i>M. stolidus sclateri</i> ^d	<i>M. oberi sclateri</i>
<i>M. oberi nugator</i>	<i>M. tyrannulus nugator</i>	<i>M. tyrannulus nugator</i>	<i>M. [tyrannulus] nugator</i>

^a Zimmer's unpublished arrangement was identical to that used by Bond (1956) except that *barbirostris* was treated as a race of *M. tuberculifer*. See footnote b.

^b In some of his later publications, Bond (1957, p. 12; 1961b, p. 10) treated *barbirostris* as a race of *M. tuberculifer*.

^c The use of brackets designates a superspecies, in the manner suggested by Amadon (1966).

^d In an earlier publication, Bond (1950, p. 98) regarded *sclateri* as a race of *M. tyrannulus*.

EXPERIMENT 142: May 14, 1966, Haiti, pair number 1 again. Tapes used, *antillarum* versus *nugator*; birds silent, location unknown at start of experiment. Start at 5:10 A.M. Within 30 seconds, both birds appeared at mid-point, then moved into *antillarum* area, calling well within 20 feet of *antillarum* model. 5:12, calling well, then in study at 8 feet from *antillarum* model. Both still in *antillarum* area at cable switch at 5:15. Within 10 seconds, both birds reoriented to new *antillarum* speaker. Then moved to mid-point, calling. 5:16, both had moved to 50 feet from *antillarum* speaker. Back to about 20 feet of *antillarum* speaker at end of experiment. Response not strong.

EXPERIMENT 143: Same conditions as in experiment 142. Tapes used, *lucaysiensis* versus *crinitus*; birds could be heard calling out of experimental area at start of experiment. Start at 5:22 A.M. No response to either experimental area during this experiment.

EXPERIMENT 144: Same conditions as in experiment 142. Tapes used, *antillarum* versus *sclateri*; both birds calling outside experimental areas at start of experiment. Start at 5:34 A.M. Both birds moved into *antillarum* area, about 30 feet from model, but not excited. One perched 8 feet from model. 5:36, one calling 15 feet from *antillarum* model, the other about 20 feet from model. No criss-crossing or passes. Remained in general *antillarum* area until cable switch at 5:39. After 1 minute, one bird reoriented to new *antillarum* speaker, perching 20 feet from new *antillarum* model. Second bird disappeared. At 5:41, one perched about 8 feet from *antillarum* model, then flew out of area. 5:42, one back to within 40 feet of *antillarum* model, but silent. Both birds in vicinity of mid-point at end of experiment at 5:44.

EXPERIMENT 145: Same conditions as in experiment 142. Tapes used, *dominicensis* versus *sclateri*; birds silent, location unknown at start of experiment. Start at 5:46 A.M. After 1 minute of silence, one bird showed in *dominicensis* area, began criss-crossing. A second bird then appeared. Birds perched at 8 feet and 10 feet from *dominicensis* model. 5:48, one in study at 8 feet, calling well. Both remained within *dominicensis* area until cable switch at 5:51. Reoriented at once to new *dominicensis* area following cable switch. Remained in *dominicensis* area, criss-crossing and passing at model for rest of experiment.

Myiarchus antillarum (Bryant)

Tyrannus antillarum BRYANT, 1866, p. 249.

Myiarchus antillarum: SUNDEVALL, 1869, p. 599. RIDGWAX, 1907, p. 638 (synonymy).

Myiarchus stolidus antillarum: COUES, 1872, p. 79. HELLMAYR, 1927, p. 169 (synonymy). BOND, 1956, p. 108.

RANGE AND SPECIMENS EXAMINED: Puerto Rico (54), Vieques (eight), Culebra, and St. Thomas and St. John (in the Virgin Islands).

The white abdomen and lack of cinnamon in the tail make this one of the most distinctive and well-defined populations within the entire genus (see key, p. 334). On strictly morphological grounds, then, there is good cause for giving it specific rank, as argued by Wetmore (1927, p. 469): "Differences between them [*M. stolidus* of Jamaica and *antillarum*] in my estimation are such as to warrant continuance of the more usual treatment of *M. antillarum* as a distinct species." The mouth lining of *antillarum* is a pale yellow like that of *sagrae* and *lucaysiensis* in the Greater Antilles and the races of *M. oberi* in the Lesser Antilles, and hence somewhat paler than the pale orange lining of *stolidus* and *dominicensis*.

From the standpoint of vocalizations, *antillarum* shows some relationship to *stolidus* and *dominicensis* on the islands to the west. Plate 29 illustrates the vocal repertoire of this Puerto Rican form. The most diagnostic vocal pattern is a fairly prolonged, plaintive, whistled note (pl. 29, fig. 6) which McCandless (1958, p. 38) characterized as "whee" and which is the basis for the local name "jüí." This whistled pattern, though of approximately the same duration as its counterpart in the repertoire of *stolidus* and *dominicensis* (pl. 27, fig. 6, and pl. 28, fig. 6), does not characteristically ascend in frequency, and on occasion will actually drop in frequency in the course of a single rendition (the last note in pl. 29, fig. 6). Consequently, the effect on the human ear is that the whistled note of *antillarum* usually sounds lower in pitch than that of *stolidus* and *dominicensis*. The only substantial difference between the "dawn song" of *antillarum* (pl. 29, figs. 1 and 4) and that of *stolidus* and *dominicensis* (pl. 27, figs. 1 and 4, and pl. 28, figs. 1 and 4) is the configuration of the terminal element. In the case of *antillarum*, the terminal element is essentially a pure, whistled note (like the introductory element), whereas it is definitely modulated in the

renditions of the Jamaican and Hispaniolan forms, in the same manner as in the "dawn songs" of *lucaysiensis* and *sagrae* (pl. 22, figs. 1 and 3 and pl. 23, figs. 1 and 3). A two-syllabled "wick-up" note (pl. 29, fig. 2), very similar to that of *stolidus* (pl. 27, fig. 2) and *dominicensis* (pl. 28, fig. 2), is a characteristic daytime pattern of *antillarum* and also is the basis for the middle element of the "dawn song," as it is with *stolidus* and *dominicensis*. A series of emphatic "huit, huit" notes (pl. 29, fig. 5), a rolling "pee-r-r-r" note (pl. 29, fig. 3), and a rasping note (pl. 29, fig. 7) constitute the remaining components of the daytime repertoire of *antillarum*.

Territorial males of *antillarum* respond positively only to playback of their own vocal repertoire and not to the repertoires of *stolidus lucaysiensis*, the races of *M. oberi*, or other congeners. No recordings of *sagrae* (like the recording of *lucaysiensis*) or of *dominicensis* (like that of *stolidus*) were available at the time of the Puerto Rican experiments in 1956. A total of 23 experiments were conducted in Puerto Rico, involving nine different territorial males of underdetermined reproductive status.

The following field notes document the entire series of eight experiments conducted with one of these pairs, and illustrate this discriminatory ability:

EXPERIMENT 84: April 25, 1965, Guánica Forest Reserve, pair number 4. Tapes used, *antillarum* versus *stolidus*; birds silent, location unknown at start of experiment. Start at 7:22 A.M. Both birds showed in *antillarum* area within 1 minute. Perched 15 feet from model, then one moved to 8 feet of model, calling well. In a study at 8 feet, giving repeated "hui" notes. Back to 20 feet, calling well. 7:27, criss-crossing *antillarum* area, giving "chew-it" calls. Cable switch at 7:29, when both were within 15 feet of *antillarum* model. Within 1 minute after switch, both birds had moved into new *antillarum* area [leaving *stolidus* voice]. 7:31, one bird within 30 feet of new *antillarum* model. Both calling excitedly, "chew-it" and rasping notes. Criss-crossing *antillarum* area, perching at 15 feet and 25 feet from model. 7:34, in study 12 feet above model, calling well. Both birds still reacting positively within a radius of 15–20 feet of *antillarum* model at end of experiment at 7:36.

EXPERIMENT 85: Same conditions as in experi-

ment 84. Tapes used, *antillarum* versus *lucaysiensis*, but position of *antillarum* speaker reversed from that at end of experiment 84; both birds still around speaker used for *antillarum* at end of experiment 84. Start at 7:39 A.M. Both birds at once reoriented to new *antillarum* area. 7:41, one perched 8 feet from model. In study at 10 feet, giving "chew-it" and rasping notes. 7:43, one in a study at 8 feet, the other 50 feet from *antillarum* model. 7:44, both within 20 feet. Criss-crossing of *antillarum* area. 7:45, one in a study, 10 feet above *antillarum* model, calling sporadically. Cable switch at 7:46. Within 1 minute, both had reoriented to new *antillarum* area. One perched at 15 feet from new *antillarum* model. Moved to 10 feet at 7:48. In a study at 8 feet. 7:50, in a prolonged study at 5 feet, while other is perched 25 feet above model. Both in study within 15 feet of *antillarum* model at end of experiment at 7:53.

EXPERIMENT 86: Same conditions as in experiment 84. Tapes used, *antillarum* versus *barbistris*, but position of *antillarum* reversed from final position in experiment 85; both birds were still in vicinity of speaker last used for *antillarum*. Start at 7:55 A.M. Both birds reoriented to new *antillarum* area within 1 minute. Criss-crossing, and one perched in study at 10 feet from *antillarum* model. 7:59, still in study at 8 feet from model. Both within 15–20 feet of *antillarum* model; one perched 4 feet from model at cable switch at 8:02. Within 1 minute following cable switch, both birds had reoriented to new *antillarum* area. One in study at 12 feet from model at 8:04. 8:06, perched at 15 feet and 20 feet from *antillarum* model. One in good study at 6 feet from model, calling sporadically. End of experiment at 8:09.

EXPERIMENT 87: Same conditions as in experiment 84. Tapes used, *stolidus* versus *lucaysiensis* [to test stimulus value of either of these repertoires, in absence of *antillarum* voice]; both birds silent, but observable outside experimental areas at start of experiment. Start at 8:11 A.M. At 8:14, both birds still observable and feeding outside experimental areas. Played back for full 7 minutes, with no response and no entry of either bird into either area. End of experiment at 8:18.

EXPERIMENT 88: Same conditions as in experiment 84. Tapes used, *antillarum* versus *stolidus* [to test stimulus value of *antillarum*, after negative response to *stolidus* and *lucaysiensis*]; birds silent and still out of experimental area at start of experiment. Start at 8:19 A.M. Both birds were back within *antillarum* area within 1 minute, calling "chew-it" and rasping notes. One perched at 8 feet from model at 8:22. 8:23, had moved to study perch at 4 feet from model. 8:25, still in study, at 10 feet from model, calling well. Cable

switch at 8:26. Both birds reoriented to new *antillarum* area within 1 minute. Criss-crossing of new area. 8:31, study at 12 feet. More criss-crossing, until end of experiment at 8:33.

EXPERIMENT 99: April 27, 1965. Same conditions as in experiment 84. Tapes used, *antillarum* versus *sclateri*; birds silent, location unknown at start of experiment. Start at 7:32 A.M. One showed in *antillarum* area within 30 seconds, perched at 25 feet from model; both birds present by 7:33, calling "chew-it's." 7:35, one at 15 feet from model, calling well. In a study at 10 feet. 7:36, both birds at about 15 feet. Criss-crossing *antillarum* area. Cable switch at 7:39. One moved into new *antillarum* area at once, passing within 3 feet of new model. Both criss-crossing in new *antillarum* area at 7:40. In a study at 10 feet from model, giving "chew-it" and rasping notes. Calling well within 30 feet of *antillarum* model for rest of experiment. End at 7:46.

EXPERIMENT 100: Same conditions as in experiment 99. Tapes used, *sclateri* versus *stolidus* [to test stimulus value of these repertoires, in absence of *antillarum*]; birds silent, location unknown at start of experiment. Start at 7:51 A.M. At 7:55, pair could be heard outside the experimental area. Observed feeding about 200 feet away. No response to either speaker. Experiment ended at 7:58, without speaker cables being switched.

EXPERIMENT 101: Same conditions as in experiment 99. Tapes used, *antillarum* versus *tuberculifer* [to test stimulus value of *antillarum* after negative response to two other repertoires in experiment 100]; birds feeding outside experimental areas at start of experiment. Start at 8:02 A.M. Both showed, calling well about 40 feet from *antillarum* model at 8:04. Criss-crossing over model at 8:06; perched at 10 feet and 15 feet from model, calling well. Criss-crossing over *antillarum* model. Cable switch at 8:09. Both at mid-point in 1.5 minutes, calling well. Both at 40 feet from new *antillarum* model at 8:13. Calling within 30 feet of *antillarum* model until end of experiment at 8:16.

Myiarchus oberi Lawrence

Myiarchus oberi berlepschii Cory

Myiarchus berlepschii CORY, 1888, p. 266.

Myiarchus oberi berlepschii: RIDGWAY, 1907, p. 620 (synonymy).

Myiarchus tyrannulus berlepschii: HELLMAYR, 1927, p. 168 (synonymy). BOND, 1956, p. 107.

RANGE AND SPECIMENS EXAMINED: St. Kitts (18), Nevis (six), and Barbuda (18).

This race is a small, northern representative of *oberi* (Dominica and Guadeloupe) from which it is nearly but not completely

separable on the basis of mensural characters (demonstrated graphically in text figs. 1 and 4). A strong morphological similarity to *M. tyrannulus* has led to its being regarded, along with most of the Lesser Antillean populations of *Myiarchus*, as an insular race of that widespread continental species (see table 6). Though *berlepschii*, as a population, averages smaller in all mensural characters than *tyrannulus* of Trinidad and Tobago, has narrower fuscous stripes in the tail, and has more prominent cinnamon edging on the secondaries than that form, some individuals cannot be identified with certainty without recourse to vocal characters. Here, then, is a prime example of how reliance upon conventional morphological taxonomy alone can lead to an erroneous concept of relationships within this difficult genus.

As Cory (1888, p. 266) suggested in his original description, *berlepschii* tends to have paler yellow under parts than does *oberi*. This color difference is extremely slight, however, and mensural characters (text figs. 1 and 4) remain the most useful means of differentiating *berlepschii* from the nominate race.

Specimens from Barbuda tend to have a slightly richer yellow on the abdomen than the birds from St. Kitts and Nevis, as pointed out by Riley (1904b, p. 287) and Ridgway (1907, p. 620), and hence are closer to *oberi* in this respect. However, nomenclatural recognition of this slight color difference would be inconsistent with the degree of divergence that one finds among the four races of *M. oberi* recognized in this revision. Ridgway (1907, p. 620) was in error in implying that Lawrence (1878, p. 239) reported on specimens of *Myiarchus* from Antigua.

The mouth lining of *berlepschii* is a pale yellow, like that of the other races of *M. oberi*, of *M. antillarum* and *M. sagrae* in the Greater Antilles, and of *M. tyrannulus* on the continent.

Perhaps the most exciting moment in my West Indian field work came in April, 1960, with the discovery that *berlepschii* is a "whistler" and hence not at all closely allied to *M. tyrannulus*, which has a vocal repertoire devoid of any pure, unmodulated, whistled notes. Subsequent field work disclosed that all four *Myiarchus* populations

north of St. Vincent (*berlepschii*, *oberi*, *sclateri*, and *sanctaeluciae*) share the same vocal repertoire. Their most diagnostic daytime vocal pattern is a prolonged, plaintive whistle, illustrated in plate 30. These whistled notes have their sound energy concentrated between 2.5 and 3.5 kilocycles, and hence are substantially lower in pitch than the whistles of *M. stolidus* or *M. antillarum* (pl. 27, fig. 6, pl. 28, fig. 6, and pl. 29, fig. 6). This difference, moreover, is very apparent to the human ear. They also average longer in duration. Variability among the whistled patterns of *berlepschii*, *oberi*, *sclateri*, and *sanctaeluciae* is comparable to what one finds among the whistles of various races within continental *Myiarchus* such as *M. tuberculifer* and *M. nuttingi*. The "dawn songs" of the races of *M. oberi*, illustrated in plate 31, show a remarkable similarity to the "dawn song" of *antillarum* (pl. 29, figs. 1 and 4), differing only in the lower frequency of the whistled components and in the configuration of the modified "wick-up" note that forms the middle element. In the races of *M. oberi* this two-syllabled "wick-up" note (pl. 32, figs. 6 and 7) differs from its counterpart in the repertoire of *stolidus* (pl. 27, fig. 2) and *dominicensis* (pl. 28, fig. 2) in that the first element descends abruptly in frequency rather than ascending initially and then falling in frequency. It is noteworthy that the "wick-up" note of *antillarum* (pl. 29, fig. 2) appears to be intermediate in this regard. Other notes within the repertoire of the insular races of *M. oberi*, including a rolling note (pl. 32, figs. 3 and 4) and the "perr-r-r" note (pl. 32, figs. 1 and 2), have their counterparts within the repertoire of *antillarum* (pl. 29, figs. 5 and 3, respectively).

Bond (1961a, 1965) seems to have been the only worker heretofore to acknowledge a difference between the vocalizations of the *Myiarchus* populations in the northern Lesser Antilles and those of the population south of St. Lucia. But he was understandably reluctant to break with the traditional taxonomic treatment followed by Hellmayr (1927) and Zimmer (MS).

Territorial males of *berlepschii* are able to discriminate between their own repertoire and that of *nugator* in the southern Lesser Antilles, that of *M. tyrannulus* of the con-

tinental, and that of all of the Greater Antillean forms. But they are unable to distinguish between their own repertoire and the repertoires of *oberi*, *sclateri*, and *sanctaeluciae*. These conclusions are based on the results of 12 experiments conducted in St. Kitts, which involved four different territorial males. The reproductive status of these birds was undetermined, though one of these pairs was in association with fledged young and was not particularly responsive.

Field notes were taken in a series of five experiments with the most responsive of these four males. These notes illustrate this discriminatory ability of *berlepschii*:

EXPERIMENT 67: April 18, 1965, 1500 feet on Molyneux Estate, pair number 1. Tapes used, *sclateri* versus *nugator*; birds silent, location unknown at start of experiment. Start at 9:40 A.M. Both birds showed in *sclateri* area by 9:43, within 30 feet of the model. Both disappeared for half a minute (chased another bird?), then returned to within 15 feet of *sclateri* model. Moved to perch 12 feet from model, but remained silent. Cable switch at 9:47. Both birds moved to mid-point immediately, then one reoriented to within 15 feet of new *sclateri* model. 9:49, both birds within 8 feet of model. Perched at 6 feet and at 12 feet from model. One moved to 5 feet of model, in study. Closest bird engaged in rather rapid criss-crossing of *sclateri* area, within 15 feet of model until end of experiment at 9:54. Both birds were silent throughout the entire experiment.

EXPERIMENT 68: Same conditions as in experiment 67. Tapes used, *sclateri* versus *antillarum* (but *sclateri* speaker reversed from position at end of last experiment); birds silent, out of experimental area at start of experiment. Start at 9:56 A.M. One bird showed in new *sclateri* area within 1 minute. 9:58, both birds within 15 feet of *sclateri* model. One "chew-it" call. Resumed criss-crossing behavior reported in last experiment. Excellent, but non-vocal response. 9:59, good pass at *sclateri* model. Some rolling and "chew-it" notes. Another pass, more criss-crossing. Cable switch at 10:03. Within 1 minute, both birds had reoriented to within 15 feet of new *sclateri* model. Some rolls and "chew-it" notes, more criss-crossing. Both left experimental area briefly (supplanted an intruder?) but returned to within 5 feet of *sclateri* model. End of experiment at 10:10.

EXPERIMENT 69: Same conditions as in experiment 67. Tapes used, *sclateri* versus *lucaysiensis* (but *sclateri* speaker opposite to position at end of experiment 68); birds silent, location unknown

at start of experiment. Start at 10:14 A.M. Within 30 seconds, one bird showed in new *sclateri* area; the other appeared by 10:15. Pass within 1 foot of *sclateri* model. Another pass. Study at 3 feet from model. Rapid criss-crossing over *sclateri* model. Cable switch at 10:21. One reoriented to new *sclateri* model in 15 seconds. Both criss-crossing *sclateri* model by 10:25. Some rolls and "chew-it" notes. A good pass. 10:27, a study from distance of 15 inches from model. End of experiment at 10:28.

EXPERIMENT 70: Same conditions as in experiment 67. Tapes used, *sclateri* versus *stolidus* (but *sclateri* speaker opposite position at end of experiment 69); birds silent, out of experimental area at start of experiment. Start at 10:31 A.M. Within 1 minute, one bird had reappeared in new *sclateri* area. 10:33, both birds within 15 feet of *sclateri* model. Criss-crossing over *sclateri* model. Some calling. Good study within 10 feet of model. One pass within 8 feet of model. Cable switch at 10:38. One reoriented immediately and assumed study at 5 feet from new *sclateri* model. Second bird at mid-point until 10:41, then joined first one in criss-crossing *sclateri* area. Some "chew-it" notes. Good study within 3 feet of model. End of experiment at 10:45. Birds became silent and disappeared.

EXPERIMENT 71: Same conditions as in experiment 67. Tapes used, *sclateri* versus *oberi* (but *sclateri* speaker placed opposite position at end of last experiment); birds silent, location unknown at start of experiment. Start at 10:48 A.M. One bird showed in *oberi* area by 10:49. Perched 5 feet from *oberi* model, then flew into *sclateri* area. Second bird appeared at mid-point at 10:51. Two birds reoriented to *oberi* area at 10:52. A third bird appeared about 40 feet from *sclateri* model. 10:54, all three birds are in *oberi* area, with one only 5 feet from *oberi* model; in a study at 6 feet. One hovered 2 feet over the *oberi* model. Cable switch at 10:55, and all three birds remained in old *oberi* area (now new *sclateri* area). Two birds in study at 30 feet from new *sclateri* model at 11:00. Two moved to mid-point briefly, then one back to *sclateri*. Both birds back to mid-point. Then one back to 20 feet from *sclateri* model; moved to 10 feet from *sclateri* model. Second bird moved back into *sclateri* area. At end of experiment at 11:02, one bird 5 feet from *sclateri* model, in a study.

Myiarchus oberi oberi Lawrence

Myiarchus oberi LAWRENCE, 1877, p. 48.

Myiarchus tyrannulus oberi: CORY, 1892, p. 14. HELLMAYR, 1927, p. 167 (synonymy). BOND, 1956, p. 107.

Myiarchus oberi oberi: RILEY, 1904a, p. 275. RIDGWAY, 1907, p. 617 (synonymy).

RANGE AND SPECIMENS EXAMINED: Dominica (28), Guadeloupe (four).

As noted in the discussion of *berlepschii*, *oberi* from Dominica and Guadeloupe has been considered by many workers as one of several Lesser Antillean representatives of the mainland *M. tyrannulus*. Though *oberi* averages slightly larger than *M. tyrannulus* (especially in bill length), and tends to have more prominent cinnamon edging on the secondaries, some individuals cannot be identified with certainty without recourse to vocal characters. I argue here that it should be considered as one race, which happens to be the nominate form, of an endemic and polytypic species of the Leeward Islands.

The mouth lining of *oberi* is pale yellow, like that of the other races of *M. oberi* and of *M. tyrannulus*, and unlike the bright orange lining of *nugator*. Mensural characters are the only practical means for discriminating between specimens of *oberi* and specimens of *berlepschii* and *sanctaeluciae* (text figs. 1-4). The color of the mouth lining, the extent of cinnamon edging to the secondaries, and vocal characters can be used to distinguish *oberi* from *nugator* (see key, p. 335).

The vocal repertoire of *oberi* is identical to that of *berlepschii*, *sclateri*, and *sanctaeluciae*, and is illustrated in plates 30-32. The diagnostic whistled notes (pl. 30, figs. 1 and 2) and "dawn song" (pl. 31, fig. 1) readily distinguish this population from *nugator* in the southern Lesser Antilles and from *M. tyrannulus* (pls. 33 and 34). As discussed in the account of *berlepschii*, there are definite similarities between the vocal repertoire of *M. oberi* and that of *M. antillarum* of Puerto Rico.

Observations and recordings were made of three territorial pairs of *oberi* on Dominica in 1963. No standardized playback experiments were conducted, but experiments conducted subsequently with *berlepschii* (see p. 355) and *sclateri* (see p. 357) demonstrated that these forms are not able to discriminate between their respective vocalizations, including those of *oberi*.

Myiarchus oberi sclateri Lawrence

Myiarchus sclateri LAWRENCE, 1879, p. 357.

RIDGWAY, 1907, p. 639 (synonymy). HELLMAYR, 1927, p. 169 (synonymy).

Myiarchus tyrannulus sclateri: BOND, 1950, p. 98.

Myiarchus stolidus sclateri: BOND, 1956, p. 108.

RANGE AND SPECIMENS EXAMINED: Martinique (14).

The type remained the only known example of this Martinique population until Peters (1927, p. 422) obtained two additional specimens. Since then, a fair sample has been accumulated but has shed little additional light on the affinities of *sclateri*. The enigma stems from the apparent morphological uniqueness of the Martinique form among the Lesser Antillean populations, i.e., it interrupts the cline of increasing body size from *berlepschii* in the north to *santaeluciae* in the south and lacks the prominent cinnamon edging of the remiges and the well-defined cinnamon stripe in the outer rectrix that characterize the other forms of the Leeward Islands. Bond's (1950, p. 98) earlier treatment of *sclateri* as a race of *M. tyrannulus*, along with the other Lesser Antillean forms, was undoubtedly influenced by geographical considerations. Subsequently both Bond (1956, p. 108) and Zimmer (MS) regarded *sclateri* as a race of *M. stolidus* of the Greater Antilles, but neither of these workers had ever heard the voice of *sclateri*, and their decision necessarily was based on general body size and rectrix coloration. My evidence indicates that it should be treated as a representative form of *M. oberi*, a polytypic species endemic to the Leeward Islands.

Morphologically, *sclateri* is closest to *stolidus* of Jamaica, but there is no problem in distinguishing these forms (see key, p. 334). The mouth lining of *sclateri* is pale yellow, like that of *berlepschii*, *oberi*, and *sanctaeluciae* in the Lesser Antilles, and like that of *M. antillarum* and the two races of *M. sagrae* in the Greater Antilles. The mouth lining of *M. stolidus* is pale orange, as noted above.

The vocal repertoire of *sclateri* (pls. 30–32) is identical to that of the other races of *M. oberi* and is discussed in the account of *berlepschii* (p. 354). The Martinique form is a "whistler," then, as implied in the local French vernacular, "*la siffleur*", and therefore has no close affinity with *M. tyrannulus* or *M. nigrator* (pls. 33 and 34). There are similarities, as noted above, between the vocal repertoire of *sclateri* and other races of *M.*

oberi, on the one hand, and the vocalizations of *M. stolidus* and *M. antillarum* on the other, which suggest a closer relationship with those Greater Antillean forms than heretofore suspected. This point is pursued in greater detail below in my discussion of the probable evolution of these insular populations.

Pinchon (1963) implied that *oberi* and *sclateri* can be differentiated by their vocalizations, but spectrographic analysis does not support this view, and the playback experiments conducted on Martinique demonstrated that territorial individuals of *sclateri* are unable to discriminate between their own vocalizations and those of *oberi* or *berlepschii*. These same experiments revealed that *sclateri* males do not respond positively to the playback of the repertoires of any of the Greater Antillean forms, including *M. antillarum* and *M. stolidus*. A total of 24 experiments were conducted in Martinique, involving nine different territorial males. The reproductive status of these birds could not be determined.

Field notes describing a series of experiments with the most responsive of these males illustrate this discriminatory ability:

EXPERIMENT 52. April 14, 1965, 1 mile north of Les Anses-d'Arlets, pair number 4. Tapes used, *oberi* versus *sclateri*; birds silent, location unknown at start of experiment. Start at 8:06 A.M. Male appeared 6 feet from *sclateri* model within 1 minute, giving rasping and "chew-it" notes. Hovered about 4 feet from model. Both birds only 6 feet from *sclateri* model at 8:09, calling well. 8:10, both still within 10 feet of *sclateri* model, calling. Cable switch at 8:13. Male still calling from perch 6 feet over new *oberi* model (formerly *sclateri*). 8:15, both birds still 20 feet from *oberi* model, calling occasionally. 8:16, both moved to 30 feet of new *sclateri* model, then to 15 feet. One bird made a pass, 5 feet from *sclateri* model. 8:18, both birds within 8 feet of *sclateri* model, calling well. One bird, perched 4 feet from model, in study, calling with rolling and "chew-it" notes. End of experiment at 8:20.

EXPERIMENT 53: Same conditions as in experiment 52. Tapes used, *sclateri* versus *crinitus* (but *sclateri* speaker placed where *oberi* speaker was at end of last experiment); male calling well in *crinitus* area (*sclateri* area at end of last experiment) at start of experiment; location of female unknown. Start at 8:21 A.M. Within 1 minute, male moved to midway, followed by a second bird. 8:24, both birds within 12 feet of new

sclateri model. Both in *sclateri* area at cable switch at 8:28. By 8:30, one bird had moved to mid-point. 8:32, male perched 15 feet from new *sclateri* model, in study, calling well. Second bird showed just before end of experiment, and both birds in *sclateri* area at end of experiment at 8:35.

EXPERIMENT 54: Same conditions as in experiment 52. Tapes used, *oberi* versus *lucaysiensis* (*oberi* speaker placed where *crinitus* speaker was at end of experiment 53); male calling in *lucaysiensis* area (formerly *sclateri* area) at start of experiment; location of female unknown. Start at 8:41 A.M. Male moved to mid-point and then to within 30 feet of *oberi* model by 8:43. 8:45, 20 feet from *oberi* model; second bird showed in *oberi* area. Both calling well. Cable switch at 8:48. Lost sight of both birds for several minutes. 8:53, one showed at mid-point, listened to the two dawn songs playing simultaneously, then flew directly to new *oberi* model. At end of experiment at 8:55, male calling well within 20 feet of *oberi* model.

EXPERIMENT 55: Same conditions as in experiment 52. Tapes used, *sclateri* versus *antillarum* (but *sclateri* speaker placed where *lucaysiensis* speaker was located at end of experiment 54); one bird calling about 30 feet from *antillarum* speaker (former *oberi* speaker) at start of experiments; location of female unknown. Start at 8:57 A.M. The calling bird had moved to mid-point by 9:01. 9:03, both birds within 30 feet of *sclateri* model, calling "chew-it" notes. Cable switch at 9:04. By 9:05 one bird had reoriented to new *sclateri* model while both dawn songs were being played simultaneously; perched 10 feet above *sclateri* model, in study, calling well. 9:09, both birds within 30 feet of *sclateri* model. End of experiment at 9:11.

EXPERIMENT 61: Same conditions as in experiment 52. Tapes used, *oberi* versus *barbirostris*; birds calling in general area before start of experiment, but exact location unknown. Start at 5:46 P.M. By 5:48, one bird showed at mid-point, then moved to *oberi* area, within 30 feet of *oberi* model, calling well. 5:51, moved to within 8 feet of *oberi* model, in study; back to mid-point, briefly, then returned to *oberi* area, just before cable switch at 5:53. Immediately after cable switch, both birds showed in the new *oberi* area. One made a pass within 6 feet of new *oberi* model. 5:55, both birds moved back to *barbirostris* area, calling within 20 feet of model; one bird moved to within 10 feet of *barbirostris* model; gradually lost interest and moved out of experimental area. End of experiment at 6:00.

EXPERIMENT 62: Same conditions as in experiment 52. Tapes used, *sclateri* versus *barbirostris* (to test stimulus value of *sclateri* to attract them back into experimental area); birds silent, out of

experimental area at start. Start at 6:02 P.M. One bird showed at mid-point within 1 minute; moved into *sclateri* area, to within 15 feet of *sclateri* model, giving "chew-it" notes. 6:05, 10 feet from *sclateri* model. Second bird showed in *sclateri* area by 6:05. Both birds calling well, 25 feet from *sclateri* model. One moved to within 8 feet, then made a pass over the model. 6:08 both within 10 feet of *sclateri* model. Cable switch at 6:09. At 6:11, one moved into new *sclateri* area, made a pass within 3 feet of new *sclateri* model; giving loud rasping notes, 20 feet from model; another pass, 4 feet over model; another pass, about 4 feet from model; both birds in *sclateri* area at 6:14, calling well. Another pass by one bird, within 10 feet of *sclateri* model. Both within 15 feet of *sclateri* model at end of experiment at 6:16.

EXPERIMENT 63: April 15, 1965. Same conditions as in experiment 52. Tapes used, *oberi* versus *sclateri*; birds silent, location unknown at start. Start at 7:40 A.M. Within 1 minute, both birds were within 20 feet of *sclateri* model, calling well. 7:43, one moved to mid-point, then back to perch 10 feet from *sclateri* model; moved up to 4 feet of model, calling well. 7:45, one flew over into *oberi* area, followed by the second bird, to within 30 feet of *oberi* model. 7:46, both birds were back in *sclateri* area, giving rolling notes. One was perched 10 feet from *sclateri* model at cable switch at 7:47. Within 1 minute, male had moved to mid-point, and both were in new *sclateri* area by 7:49. Both back into *oberi* area, and within 20 feet of *oberi* model. 7:52, both had reoriented to *sclateri* area, perching 30 feet from model. Had moved to 20 feet from *sclateri* model at end of experiment at 7:54.

EXPERIMENT 64: Same conditions as in experiment 63. Tapes used, *sclateri* versus *stolidus*; birds silent, just outside what was the *sclateri* area at end of last experiment, but now is the *stolidus* area. Start at 7:56 A.M. Birds began giving rolls and rasping notes. 7:58, one showed at mid-point; had moved to 25 feet of new *sclateri* model by cable switch at 8:03. Within 30 seconds, both birds were within 20 feet of new *sclateri* model, calling well. 8:08, both left perches to go to mid-point briefly, then moved back into *sclateri* area; one made a pass within 4 feet of *sclateri* model. End of experiment at 8:10.

EXPERIMENT 65: Same conditions as in experiment 63. Tapes used, *stolidus* versus *antillarum*; birds silent, location unknown at start. Start at 8:13 A.M. At 8:17, heard the pair calling on slope above us, more than 100 feet away. Spotted one of them perched quietly about 100 feet from each model, at 8:19. Then spotted both in same tree. Cable switch at 8:20, and both birds flew over *stolidus* area and then out of sight. Had not

entered experimental area by end of experiment at 8:27.

EXPERIMENT 66: Same conditions as in experiment 63. Tapes used, *oberi* versus *antillarum* [to test stimulus value of *oberi* after negative response in experiment 65]; birds out of experimental area at start. Start at 8:29 A.M. By 8:35, one bird showed at mid-point, giving rasping note. Cable switch at 8:36. Both birds back in experimental area by 8:37. 8:38, one moved to within 10 feet of new *oberi* model, giving roll note; made a pass within 3 feet of *oberi* model. Both birds remained in *oberi* area until end of experiment at 8:43.

Pinchon (1963) has suggested that *sclateri* may build a cuplike nest in the fork of a branch, rather than using a cavity as do all other species of *Myiarchus*, but admitted that this point needed verification. When in Martinique in 1960 I queried Père Pinchon on this point and learned that the basis for his suspicion was an observation of *sclateri* fledglings being fed by adults near an open nest. Unfortunately, I was unable to find a *sclateri* nest cavity during my field work in Martinique, but I have no doubt that this population has the same nesting habits as those that typify the entire genus.

Myiarchus oberi sanctaeluciae

Hellmayr and Seilern

Myiarchus tyrannulus sanctae-luciae HELLMAYR AND SEILERN, 1915, p. 201. HELLMAYR, 1927, p. 168 (synonymy). BOND, 1956, p. 107.

Myiarchus oberi oberi: RIDGWAY, 1907, p. 617.

RANGE AND SPECIMENS EXAMINED: St. Lucia (30).

The St. Lucian form is a large, well-defined southern representative of *oberi*, nearly but not completely separable from that form on the basis of mensural characters (text figs. 1-4). Like *berlepschii* and *oberi*, *sanctaeluciae* has a pale yellow mouth lining and prominent cinnamon edging to the secondaries, and these characters serve to distinguish the St. Lucian population from *nugator* to the south. The large size of *sanctaeluciae* at once separates it from *M. tyrannulus* of South America, with which it has been allied by most workers (see table 6).

The vocal repertoire of *sanctaeluciae* is identical to that of the three races of *M. oberi* to the north (*sclateri*, *oberi*, and *berlep-*

schii), as illustrated in plates 30-32. Its diagnostic plaintive whistle (pl. 30, figs. 3 and 6) and "dawn song" (pl. 31, figs. 2 and 4) at once distinguish it from the raucous notes of *nugator* and *M. tyrannulus* (pls. 33 and 34). Observations and recordings were made of three pairs of *sanctaeluciae* in 1966. No standardized playback experiments were conducted, in view of the results obtained from experiments with *sclateri* and *berlepschii* which have identical vocal repertoires.

Myiarchus nugator Riley

Myiarchus oberi nugator RILEY, 1904a, p. 275. RIDGWAY, 1907, p. 619 (synonymy).

Myiarchus tyrannulus nugator: HELLMAYR, 1927, p. 167 (synonymy). BOND, 1956, p. 107.

RANGE AND SPECIMENS EXAMINED: Grenada (10), the Grenadines (26), and St. Vincent (32).

The presence of extensive cinnamon in the tail and a general conformity in size have been the principal bases for the alignment of this form from the extreme southern Lesser Antillean islands with *M. oberi* in the northern Lesser Antilles (Cory, 1889; Riley, 1904a; and Ridgway, 1907) and with *M. tyrannulus* of South America (Sclater 1888; Clark, 1905; Hellmayr, 1927; and most recent workers, including Zimmer, MS; and Bond, 1956). I argue here that it should be considered an endemic and monotypic species of the Windward Islands.

Among the West Indian forms, *nugator* is most similar morphologically to three races of *M. oberi* (*berlepschii*, *oberi*, and *sanctaeluciae*), but differs from those forms in having (1) a bright orange mouth lining instead of pale yellow and (2) most of the secondaries fringed with smoke gray or pale cream rather than cinnamon. Among the South American forms, *nugator* is nearest to *M. t. tyrannulus* of Trinidad and Venezuela and to *M. tyrannulus tobagensis* of Tobago, but averages a longer bill and more cinnamon in the tail than those forms. Fresh specimens of *nugator* are readily separable from *M. tyrannulus* by the bright orange, rather than pale yellow, mouth lining.

Since there is no evidence of infraspecific variation in color of mouth lining among continental forms of *Myiarchus*, the treatment of *nugator* as an insular representative of the

widespread continental species *M. tyrannulus* appears unwarranted. This position becomes completely untenable when one compares their vocalizations and the responses of territorial males to playback of their respective vocal repertoires.

As is demonstrated above, the most diagnostic vocal pattern of all other Lesser Antillean populations of *Myiarchus* is a prolonged, plaintive whistle. There is no such unmodulated, whistled pattern in the repertoire of *nugator* (pl. 33); consequently, the "dawn song" of *nugator* is also very different from that of the insular forms to the north (compare pls. 34 and 31). However, a comparison of the "dawn songs" of *nugator* with those recorded from various populations of *M. tyrannulus* in Middle and South America (pl. 34) reveals a remarkable similarity which, in accordance with a general similarity in size and in plumage coloration and pattern, supports the conclusion from morphological data that *nugator* is closely related to *M. tyrannulus*. But there are other portions of the vocal repertoires of *nugator* and *M. tyrannulus* that are different, and this divergence is most evident in the pattern of the loudest, most raucous, daytime call characteristic of each form (pl. 33, figs. 1-3). The graphs in plate 33, figures 4 and 5, are of this same call but were produced with the wide band-pass filter to improve the resolution in time. The displays resulting from this technique suggest that the rate of modulation in this call is much greater in *M. tyrannulus* than in *nugator*. This degree of vocal divergence in a diagnostic call such as this is greater than is found at the subspecific level within continental forms in this genus.

Territorial males of *nugator* are able to discriminate between their own vocal repertoire and those of *M. tyrannulus* and all West Indian species of *Myiarchus*, as revealed by a total of 41 field experiments conducted in Grenada. These playback experiments were conducted at 11 different locations and presumably involved 11 different territorial males, though none of the birds were individually marked. Two of these males were paired with females that were known to be incubating, and one male was feeding young in the nest. The breeding status of the remaining males was not determined. Of the

11 males, nine demonstrated consistently positive responses, though of varying degrees, to the playback of *nugator* vocalizations, and negative responses to the playback of other *Myiarchus* repertoires, including that of *M. tyrannulus*.

The descriptive notes taken in the field of a series of experiments with one pair illustrate this ability of *nugator* males to discriminate between their own vocal repertoire and those of congeners.

EXPERIMENT 13: April 2, 1965. True Blue Estate, 2.25 air miles due east of the Point Saline lighthouse; pair number 4, female incubating; speakers placed 100 feet apart, on opposite sides of nest tree. Tapes used, *nugator* versus *tyrannulus*; birds silent, location unknown at start of experiment. Start at 10:20 A.M. Male showed in nest tree at once, calling well. 10:23, both birds oriented to within 15 feet of *nugator* speaker. Both birds calling and taking positions near *nugator* speaker, once as close as 2 feet from the model. Cable switch at 10:27. By 10:30, both birds had reoriented to new *nugator* site (opposite side of nest tree), leaving voice of *tyrannulus*. 10:30:30, both birds were oriented within 6 feet of *nugator* speaker. One bird perched 4 feet from model, calling well. End of experiment at 10:34.

EXPERIMENT 14: Same conditions as in experiment 13. Tapes used, *nugator* versus *lucaysiensis* (*nugator* speaker now where *tyrannulus* speaker was at end of experiment 13). Start at 10:40 A.M. Male calling well in nest tree, oriented toward *nugator* speaker within 30 seconds; perching 30 feet on other side of speaker from nest tree. 10:42, male perched only 10 feet from *nugator* model. Male made a pass at the model, then perched 10 feet on other side of model. 10:43, male perched 2 feet from model, male made another pass at model. 10:44, male returned to nest cavity, female perched outside cavity, then both birds flew to *nugator* area. Cable switch at 10:47. Within 1 minute, male flew past nest tree to new *nugator* speaker, passed within 3 feet of new *nugator* model; male perched 3 feet from model. 10:49, another pass within 6 feet of model; male flew up to nest cavity, joined female there [she had left experimental area in interim]. Male supplanted an intruding *nugator*, but back to *nugator* model by 10:55. Male perched 10 feet from model; moved to perch 3 feet from model, calling well; pass at model, within 3 feet. End of experiment at 10:54.

EXPERIMENT 15: Same conditions as in experiment 13. Tapes used, *barbirostris* versus *sclateri*. Start at 10:57 A.M. Both birds near nest cavity.

Several attempted copulations within 4 feet of nest cavity. Both birds remained in and around nest cavity throughout 7 minutes of playback; no response to either speaker. Experiment ended at 11:04, without switching cables or continuing with second half of experiment.

No further experimentation was conducted with pair number 4 until two days later, when another series of three playback experiments were performed.

EXPERIMENT 23: April 4, 1965. Same conditions as in experiment 13. Tapes used, *nugator* versus *tyrannulus*; birds silent, location unknown at start of experiment. Start at 6:02 A.M. Male showed at once, in *tyrannulus* area, calling well. Female appeared from nest cavity at 6:03, and both birds at once oriented to *nugator* area, perched about 20 feet from model, calling repeatedly. 6:05, back to nest tree at mid-point, still calling well. Male then returned to *nugator* area, perched 10 feet from model at 6:06. Cable switch at 6:09, at which time female was still in nest tree at mid-point, and male was still in *nugator* area. Within 1 minute, male reoriented to new *nugator* speaker. At 6:11, both birds now 75 feet on side of *nugator* speaker away from nest tree. 6:12, male perched within 2 feet of *nugator* model, calling repeatedly. 6:14, female back in nest tree, male calling 30 feet from *nugator* model. End of experiment at 6:16, at which time both birds were back in nest tree, still calling well. Within 30 seconds after cessation of tapes, both birds were again silent.

EXPERIMENT 24: Same conditions as in experiment 23. Tapes used, *tyrannulus* versus *oberi*; birds silent, location unknown at start of experiment. Start at 6:18 A.M. Birds became vocal at once. Male perched within 20 feet of *tyrannulus* model, but then became quiet, and dropped back to 40 feet from model. 6:20, one bird returned to nest tree, and other calling about 100 feet beyond experimental area. 6:23, male picked up a berry and fed it to female at point 40 feet from *tyrannulus* speaker. Showing no further interest in *tyrannulus* model. Cable switch at 6:25, and birds are silent. 6:27, male left tree where feeding on berries, perched 15 feet from new *tyrannulus* model, calling, but 1 minute later it returned to nest tree toward ground with female, and thence off into scrub. At 6:30, neither bird could be heard, location uncertain. 6:31, female returned to nest cavity, male calling softly 40 feet behind *oberi* speaker. End of experiment at 6:32, with no consistent response to either speaker.

EXPERIMENT 25: Same conditions as in experiment 23. Tapes used, *nugator* versus *oberi* (*nugator* speaker at location where *oberi* speaker was in

experiment 24); male in nest tree but silent. Start at 6:36 A.M. Male began calling at once, female came out of nest cavity. Male oriented toward *nugator* speaker and made a pass within 4 feet of *nugator* model. 6:38, male passed within 3 feet of model, perched 10 feet from mount, calling well. 6:40, male still perched 10 feet from mount, in study, calling well; then female joined the male at same spot, both calling well. Male made a pass at model at 6:41, and another pass at 6:42, to within 1 foot of model; both birds still calling well. One bird hovered 3 inches from *nugator* model. Another pass within 1 foot of model. Cable switch at 6:43. Both birds reoriented to new *nugator* area, calling from perch 20 feet from model. 6:45, female returned to nest cavity, and male returned to nest tree, calling well. 6:47, female appeared from cavity again, and both returned to *nugator* area, calling repeatedly, 30 feet from model. 6:50, one 30 feet from model, the other 20 feet from *nugator* model, calling well. One moved to within 5 feet of model, in study. One made a pass at the model, within 1 foot. End of experiment at 6:50.

Two of the 11 males with which I experimented in Grenada demonstrated inconsistent and mixed responses to the simultaneous playback of *nugator* and *tyrannulus*. These birds apparently occupied adjacent territories and inadvertently the location of experiments 36 and 37 apparently coincided with the boundary between their respective territories. This fact may, in part, be responsible for the mixed responses.

EXPERIMENT 36: April 5, 1965. Quarantine Station, 2.75 air miles northeast of the Point Saline lighthouse; pair number 9, breeding status undetermined. Tapes used, *nugator* versus *tyrannulus*; birds silent, location unknown at start of experiment. Start at 9:06 A.M. After 2 minutes, one bird showed at mid-point, then oriented toward *tyrannulus* speaker, where joined by a second bird; both within 8 feet of *tyrannulus* model. 9:09, had moved to within 3 feet and 2 feet of model, but silent. 9:10, a third bird appeared in *tyrannulus* area, 8 feet from model. 9:11, two of the three birds left, while the third remained within 4 feet of *tyrannulus* model. Cable switch at 9:13. At once this bird reoriented to the new *tyrannulus* speaker [thereby leaving the voice of *nugator*] and perched about 30 feet from the new *tyrannulus* model, but remained silent. A second silent bird appeared in *tyrannulus* area at 9:16. One of these moved to 5 feet from *tyrannulus* model at 9:17; no activity in *nugator* area. 9:19, one bird moved over to *nugator* area and perched 8 feet from

model, but remained silent; moved to within 4 feet of model, still silent. End of experiment at 9:20.

EXPERIMENT 37: Same conditions as in experiment 36. Tapes used, same as in experiment 36, but positions reversed; one of the birds perched only 8 feet from what was the *nugator* model at the end of experiment 36, but is to be the *tyrannulus* model in this experiment. Start at 9:22 A.M. Within 1 minute, the bird perched near the *tyrannulus* model reoriented to the new *nugator* speaker; perched at 20 feet from model, then moved in to 4 feet from model, still silent; back to 10 feet, in study. 9:26, two additional birds moved into the *nugator* area, one of whom was calling well. First bird supplanted by one of the newcomers (the vocal one). The vocal newcomer dropped down to within 3 feet of *nugator* model, calling well, and accompanied by a silent bird, presumably the female. Cable switch at 9:29. Male still calling well 8 feet from *nugator* model at the switch. Within 1 minute, both birds moved back to 30 feet from what is now the *tyrannulus* model. At 9:32, both birds had reoriented to new *nugator* model, perching 10 feet away, and calling well. One moved to within 2 feet of *nugator*

model, calling repeatedly; a good study, with much calling. 9:34, both birds within 5 feet of model; male chased female in aerial maneuver to mid-point, still calling excitedly. Perched at mid-point at 9:35; both birds moved back into *nugator* area, still calling. Both birds about 30 feet from *nugator* model at end of experiment at 9:36.

Experiments 38 and 39 were conducted at a location about 200 feet from where experiments 36 and 37 were performed, with the intent of possibly demonstrating a better response from pair number 10, and eliminating the potential interference of the birds of pair number 9, but there was an inconsistent and mixed response from pair 10 as well. On the basis of the experimentation with pairs 9 and 10, it would be difficult to demonstrate any consistent ability of *nugator* to discriminate between its own vocal repertoire and that of *tyrannulus*. The impressive responses of the other nine territorial males provide, however, substantial proof of this ability.

PROBABLE EVOLUTION OF WEST INDIAN *MYIARCHUS*

ZOOGEOGRAPHERS (Myers, 1938; Bond, 1948 1963; Simpson, 1956; Darlington, 1957) have given substantial support to the theory that the West Indian islands are oceanic, with no geological history of continental land connections. The implication follows that all colonization of these islands was achieved by over-water dispersal, perhaps aided to some extent by tropical storms. Bond (1948, p. 227) has concluded that "the prevailing easterly trade winds have had little effect on bird distribution." As Darlington has stated (1938), "the fauna is an accumulation of immigrants, not the residue of a continental fauna."

According to Bond (1934, 1948, 1963) and Mayr (1946), most of the avifauna of the West Indies had its origin in tropical (= southern) North America which includes Central America. The South American element is of comparatively recent arrival and comprises only members of the distributionally more aggressive families. The West Indian distribution of *Myiarchus*, a representative of the largest and most aggressive of South American suboscine families (Tyrannidae), supports this view and is discussed in some detail here.

In working out the present and past distribution of a group of tyrant flycatchers such as *Myiarchus*, we need not be concerned with the problem of human transport and introduction. These birds are not prized for either their beauty or their song, and are notoriously difficult to maintain in captivity. But there is one major disadvantage in working with such a group, as with most elements of any avifauna, i.e., the nearly complete lack of fossil material. There are no published reports of fossil remnants of *Myiarchus* flycatchers.

There is general agreement among most avian paleontologists that most genera and many of the well-defined species of our present day avifauna were well established by the beginning of the Pleistocene, and that modifications throughout the Pleistocene and during Recent times have been mainly at the level of the less well-defined species and geographical races (Howard, 1950; Wetmore,

1959; Brodkorb, 1960). In working late Pleistocene deposits in the Bahamas, Brodkorb (1959) had identified the fossil remains of two species of small land birds that are represented in the present-day West Indian avifauna and are specifically distinct from mainland relatives (a woodpecker, *Melanerpes superciliaris*; and a mockingbird, *Mimus gundlachi*). Bernstein (1965), reporting on a late Pleistocene deposit in the Dominican Republic, listed fossil remains that could not be distinguished from a number of present-day species endemic to the island of Hispaniola: both species of endemic todies (*Todus*), two woodpeckers (*Melanerpes* and *Nesocittes*), a palm tanager (*Phaenicophilus*) and the palm chat (*Dulus*).

Late Pleistocene fossils of two genera (*Contopus* and *Tyrannus*) of tyrannid flycatchers have been found in the West Indies (Bernstein, 1965). Fossil remains have been found in late Pleistocene deposits of the southern United States which cannot be distinguished from such present-day tyrannids as *Tyrannus tyrannus* (Brodkorb, 1957), *Contopus virens* (Wetmore, 1962), and *Sayornis phoebe* (Wetmore, 1962). It is perhaps reasonable to assume that the better-defined West Indian populations of *Myiarchus*, i. e., those that differ most from mainland forms or from other Antillean forms, probably reached the islands before or at the beginning of the glacial periods, a million years ago. The source of these earliest invaders was almost certainly the late Tertiary avifauna of Central America.

Simpson (1956) has written that the "Central American faunas, and particularly those of the Honduras and Yucatan projections, were almost completely North American until the late Pliocene," when a land bridge was re-formed with South America after many millions of years of separation. But, as Mayr (1946) has pointed out, it is unlikely that some South American families of birds, including the tyrant flycatchers, would have been totally restricted from invading Central America by a Central American water gap. Those genera of Tyrannidae that now range as far northward as Canada (*Tyrannus*,

Myiarchus, *Contopus*, *Empidonax*, and *Sayornis*) may well have become established in Central America before the continents were connected, perhaps several million years ago. Significantly, all these genera except *Sayornis* have successfully invaded the West Indies, indicating a strong propensity for over-water dispersal and colonization. Bond (1963) has concluded that "most of the Antillean tyrannids were derived from Central America, but some of the Lesser Antillean species . . . are more or less recent arrivals from the south [=South America]." My conclusions regarding the probable evolution of *Myiarchus* in the West Indies would support this viewpoint.

An analysis of the distribution of the present-day populations of West Indian *Myiarchus*, following the specific limits recommended here, suggests that there may have been four primary invasions of the Antillean region by mainland forms of *Myiarchus* (numbered arrows in pls. 35 and 36). The most easily interpreted of these four invasions is also unquestionably the most recent. *Myiarchus nugator*, in the southern Lesser Antilles, would appear to be a late Pleistocene derivative of *M. tyrannulus* of Trinidad and the South American Continent (pl. 36). Though little differentiated from *tyrannulus* with respect to size and plumage coloration and pattern, *nugator* did develop a differently colored mouth lining and a vocal repertoire sufficiently distinct to result in discrimination by territorial males, which entitle it to specific rank. It is noteworthy that during the evolution of *M. nugator* from *M. tyrannulus* the so-called "dawn song" of the newly emergent species has resisted change to the extent that it is virtually inseparable from that of the parent stock on the continent.

There is no close relationship between *M. nugator* and the other West Indian populations of *Myiarchus*. My revision of the specific limits and affinities of the Lesser Antillean populations of *Myiarchus* becomes especially critical in any zoogeographical interpretation of the avifauna of that region. Voous (1955, p. 13), for example, used the presence of *Myiarchus* "*tyrannulus*" in the Antilles "as far north as St. Kitts" as proof of "its way of colonization from the South American continent northward." It now becomes clear that "*tyrannulus*," or, more

accurately, its recent derivative *M. nugator*, has been successful in its northward colonization only as far as St. Vincent (pl. 36). Though there is no evidence that there has ever been a land connection between Venezuela and Grenada, even during the glacial periods, the water gap may have been reduced to no more than 20 miles. An over-water invasion of Grenada by mainland *tyrannulus* no doubt resulted in small, isolated colonies and the subsequent colonization of the Grenadines and St. Vincent probably was extremely slow. Probably *nugator* did not reach St. Vincent until after the last glacial retreat and the formation of an effective barrier (80 miles of water) between Grenada and Trinidad. By that time a water barrier, nearly 30 miles wide, would have prohibited the northward spread of this young species to St. Lucia, where it would have had to compete with another species of *Myiarchus* that had come down from the north, namely, *M. oberi sanctaeluciae*.

Bond (1963) has estimated that approximately 33 "land birds" (only 15% of the West Indian avifauna, Columbiformes through Passeriformes) have entered the West Indies directly from South America, via Grenada. It is noteworthy that nearly half of this group, like *M. nugator*, has not penetrated north of St. Vincent. Another flycatcher, *Elaenia flavogaster*, is among those the range of which terminates there. Its invasion may have been more recent than that of *Myiarchus nugator*, however, for *E. flavogaster* is not specifically distinct from a widespread taxon in Middle and South America. As in the case of *M. nugator*, *E. flavogaster* comes into potential competition with a sibling species that is firmly established to the north (*E. martinica*). Other relatively recent arrivals from South America that have not spread north of the southernmost Lesser Antilles include another flycatcher (*Tyrannulus melancholicus*), a thrush (*Turdus fumigatus*), a tanager (*Tangara cucullata*), and two finches (*Sporophila nigricollis* and *Volatinia jacarina*). This zoogeographical pattern is also illustrated in the mammalian fauna of the southern Lesser Antilles which Simpson (1956) regarded as "a highly attenuated extension of the recent fauna of Trinidad and eastern Venezuela."

Jamaica is the only island in the West In-

dies on which more than one species of *Myiarchus* is found, and there is reason to believe that this island has served as the only other successful primary pathway of entry for the genus. This route has apparently been followed by a number of West Indian birds that presumably reached Jamaica from the Honduran-Nicaraguan bulge. Most Jamaican endemics, including *Platyptaris niger* and *Myiopagis cotta*, are representatives of Middle American genera, and there is no reason to believe that they ever occurred elsewhere in the Antillean region. Likewise, it seems highly improbable that the two endemic Jamaican species of *Myiarchus* (*M. validus* and *M. barbirostris*) are present-day relicts of species that formerly were widespread in the Antillean region. If they are autochthonous in Jamaica, as I believe, they must be considered derivatives of two species of *Myiarchus* from the Pleistocene fauna of Middle America. An earlier arrival would have permitted these forms to spread to the other Greater Antillean islands at a time when the water gaps between the islands were narrowest or possibly closed by land bridges and hence probably can be ruled out (Darlington, 1938, p. 298).

It seems clear that *M. barbirostris* has been derived from *M. tuberculifer* of Middle America, as the result of a relatively recent invasion, perhaps as recent as the mid or late Pleistocene (pl. 36). The degree of divergence in morphology and vocalizations has been somewhat greater in this instance than occurred in the evolution of *M. nugator* from *M. tyrannulus*.

The source of *M. validus* is now completely obscure, but presumably it was a member of the early Pleistocene avifauna of Middle America. The invasion of Jamaica by *proto-validus* must have been early enough to provide sufficient time for obliteration of a close affinity with any of the mainland species of *Myiarchus*, yet not so early as to have enabled it to take advantage of the narrower water gaps between the islands and thereby extend its range within the West Indies (pl. 36).

I believe a rationale can be developed to explain the derivation of all the remaining West Indian species of *Myiarchus* from a common ancestral form, the prototype of *stolidus*, the third Jamaican species. The

source of this early pioneer, as in the case of *proto-validus*, is now obscure. Unlike the case of *barbirostris*, there is no convincing evidence, either morphological or vocal, to link *stolidus* with any present-day species in Middle America. But *proto-stolidus* must have reached Jamaica as the result of the earliest of the four primary invasions (pl. 35), perhaps during the late Pliocene, which would have permitted it to spread throughout the Greater Antillean region during the period prior to the submergence of the land masses to their present levels.

Since it was the only hole-nesting flycatcher in Jamaica during its early evolution, *proto-stolidus* may have been successful to the point where there was populational pressure toward exploitation of the same unoccupied niche elsewhere within the Greater Antillean region. Geologists are not in agreement as to what extent or in what manner Jamaica, Hispaniola, and Cuba were connected, if at all. However, Darlington (1938, pp. 294-296) has interpreted faunal relationships among these islands as evidence that the linkage has been primarily from Jamaica to Hispaniola to Cuba, and this theory would apply very nicely to *Myiarchus*. It seems likely that Jamaica and Hispaniola were connected, or nearly so, at the time that *stolidus* was evolving from the original invading stock, for *dominicensis* of Hispaniola and *stolidus* of Jamaica share the same vocal repertoire and color of mouth lining and are only slightly divergent in their plumage coloration and pattern.

There are other probable immigrants from Central America that may have used Jamaica as their route of entry into the West Indies and then spread to other Greater Antillean islands. It is noteworthy that some of these, including *Elaenia fallax* and *Nyctibius griseus*, are found only on Jamaica and Hispaniola, which further suggests a closer faunal link between those islands than between Jamaica and Cuba. An endemic Antillean nightjar, *Siphonorhis*, "is apparently related to the widespread continental *Nyctidromus*. Its range in the Greater Antilles (Jamaica, Hispaniola and Gonave Island) indicates derivation from the West" (Bond, 1963). Other probable Middle American derivatives of the West Indian avifauna, such as *Porzana flaviventer* and the parrot genera

Aratinga and *Amazona*, are (or were) present on all the Greater Antillean islands. The species of *Amazona* in Cuba, Jamaica, and Hispaniola show an interesting parallel to the *M. stolidus* group in the same islands. They comprise a superspecies which is closely related to *A. albifrons* of Central America and no doubt was derived from that form. The Jamaican member of the superspecies is more closely related to the Hispaniolan member than to the Cuban member (Bond, 1956), and Jamaica is the only island with more than one species of *Amazona*.

The subsequent spread of *Myiarchus* from Hispaniola apparently occurred in two different directions, though almost certainly at two different time levels (pl. 35). It is noteworthy that both of these later invasions, one into Cuba and the other into Puerto Rico, resulted in the loss of the yellow pigmentation on the under parts, a reduction of the cinnamon coloration of the tail, and a paling of the mouth lining in the two emergent species (*M. sagrae* and *M. antillarum*).

The invasion of Cuba by proto-*sagrae* must have been early enough to permit not only the loss of pigmentation noted above, but also a loss of the unmodulated whistled note that is so characteristic of *dominicensis*. Except for the loss of the initial whistled component, the "dawn song" of *sagrae* has been quite conservative and remained indistinguishable from that of *dominicensis*. That *lucaysiensis* of the Bahamas should be only subspecifically distinct from *sagrae* is not surprising, for its development would have had to be quite recent, following the emergence of the Bahaman islands during the Pleistocene (Schuchert, 1935). In general, the avifauna of the Bahamas (Chapman, 1891; Bond, 1948) as well as the bat fauna (Koopman, Hecht, and Ledecy-Janacek, 1957) appears to have been derived from Cuba rather than from Hispaniola. The Grand Cayman population is not yet separable from *sagrae* of Cuba and must be the result of a very recent invasion. Bond (1950) has noted that "evidently more Cayman birds have been derived from Cuba than from Jamaica."

The evolution of *antillarum* in Puerto Rico, due to an early invasion from Hispaniola (pl. 35), involved the loss of pigmentation

noted above and some divergence in vocalizations, though not to the degree that occurred with *sagrae*. The diagnostic whistled note was retained but altered somewhat from that of *dominicensis*, and the terminal component of the "dawn song" became a pure, whistled note, unlike the modulated note of *dominicensis* and *sagrae*.

It now seems probable that the populations of *M. oberi* in the northern Lesser Antilles have their closest relative in *M. antillarum* of Puerto Rico, though this relationship had not been suggested by previous workers and is anything but obvious on morphological grounds. The fact that they are "whistlers" and have a "dawn song" that differs from that of *antillarum* primarily in its lower frequency suggests that they evolved as a consequence of a series of range extensions from original Puerto Rican stock, beginning with the crossing of the Anegada Passage between the Virgin Islands and the Leeward Islands and terminating with the colonization of St. Lucia (pl. 35). Most of these colonizations would have had to be over-water dispersal for the Lesser Antillean islands north of St. Vincent probably have never been connected, though on this point geologists differ (Schuchert, 1935).

The smaller, northern Lesser Antillean islands undoubtedly have been an effective barrier to the further range expansion of many Greater Antillean species, but there is evidence that some Lesser Antillean birds other than *Myiarchus* have had their origin in the Greater Antilles. For example, *Geotrygon mystacea* of the northern Lesser Antilles "was clearly derived from, and is often considered conspecific with, the Greater Antillean *G. chrysia* . . . it has spread south to St. Lucia, but has never been reported from the southernmost islands" (Bond, 1963). *Myadestes genibarbis* undoubtedly was derived from a Middle American form and subsequently spread from the Greater Antilles through the Lesser Antilles and is common in the mountains as far south as St. Lucia. The West Indian populations of the flycatcher genus *Contopus* almost certainly originated from Central American congeners and subsequently spread throughout the Greater Antilles and down the Lesser Antilles as far as St. Lucia. It is noteworthy that the

Puerto Rican population (*C. latirostris blancoi*) is more similar to the Lesser Antillean forms (*C. latirostris brunneicapillus* and *C. l. latirostris*) than to the other Greater Antillean members of the genus (*C. caribaeus* subsp.). Antillean grackles of the genus *Quiscalus* (= *Holoquiscalus*) appear to have been derived from Central America and then spread eastward and southward through the Lesser Antilles. The presence of a race of the Lesser Antillean species (*Q. lugubris*) in northern South America "presumably resulted from an invasion of that continent by this species from the Lesser Antilles" (Bond, 1963), though the apparent rarity of island-to-continent invasions gives one pause. Likewise, the Lesser Antillean populations of *Icterus* are assumed to have been derived from Central American stock by way of the Greater Antilles (Bond, 1963).

In its evolution from *M. antillarum*, *M. oberi* reverted to the yellow pigmentation of the under parts and the cinnamon coloration in the tail that had been lost in the transition from *dominicensis* to *antillarum*, but maintained the pale yellow mouth lining and the trend toward larger size established in Puerto Rico. The development of the four representative and potentially interbreeding populations of *M. oberi* must have been relatively recent and rather rapid (pl. 35). These forms have extremely sparse populations which may in part be attributed to the scarcity of suitable nesting cavities. Only one of the four populations (*oberi* on Guadeloupe), for example, has access to woodpecker holes. Low population density in conjunction with the small size of the islands involved may have promoted a rapid evolution of the isolates, as suggested for other groups. The significant point here, from the standpoint of the systematics of *Myiarchus*, is the lesson to be learned with respect to the *relative* inconstancy of such morphological characters as body size, rectrix pattern, and coloration of the under parts, in contrast to the conservativeness of certain vocalizations, especially the so-called "dawn song." This could be construed as circular reasoning, having used this trenchant attribute of voice to establish the specific limits and affinities of *M. oberi* to begin with, yet we find similar evidence when we compare populations within such wide-

-ranging and polytypic continental species as *M. tuberculifer* and *M. tyrannulus*, in which vocalizations surely play a significant role in reproductive isolation (Lanyon, 1963a).

The apparent morphological uniqueness of *M. oberi sclateri* with respect to the populations north and south of Martinique has been the source of some embarrassment to those persons who have tried to establish its affinities without violating zoogeographical principles. Bond (1934), in discussing the peculiar presence of such distinct forms, expressed the belief that "the present island of Martinique is older geologically than the remainder of the Lesser Antilles, and that the peculiar species of the island represent older types," implying that forms such as *sclateri* may have arrived at an earlier date and independently from related birds to the north and south. In view of the current evidence for (1) treating *sclateri* as a potentially interbreeding and representative form of the polytypic Lesser Antillean *M. oberi*, and (2) considering *M. oberi* as a direct descendant from *M. antillarum* of Puerto Rico, it seems highly improbable than an independent invasion of Puerto Rican birds into Martinique could have produced a taxon with a vocal repertoire identical to that of three other taxa that evolved via the Virgin Islands. Furthermore, such a theory would necessarily imply that *M. o. sanctaeluciae* reached St. Lucia by still another independent invasion from Puerto Rico or by "leap-frogging" over Martinique from Guadeloupe. The series of progressive range extensions indicated in plate 35 would seem to be the more reasonable hypothesis to explain the evolution of all the populations of *M. oberi*.

In order not to obscure the close relationship between the various populations of *M. oberi* and the Greater Antillean species of *Myiarchus*, and at the same time afford the Lesser Antillean group its recognition as a distinct species, it would be advisable to evoke the superspecies concept here, as indicated in table 6. This procedure would also emphasize that the path of entry of the *oberi* group was from the west rather than from the south as has generally been believed to be the case heretofore. The oldest available name within this assemblage, *stolidus*, should be used to designate the superspecies.

SUMMARY

THE EXTENT OF MORPHOLOGICAL and vocal divergence among West Indian populations of *Myiarchus* is documented, and a key to the identification of these flycatchers is included. Of the 12 recognizable taxa, seven species (all endemic) are admitted. No new forms are recognized, but substantial changes in specific limits are recommended, based principally on the response of territorial males to the playback of vocal repertoires: four monotypic species, including two on Jamaica (*M. validus* and *M. barbirostris*), one on Puerto Rico (*M. antillarum*), and one in the southern Lesser Antilles (*M. nugator*); three polytypic species, including one on Cuba, Grand Cayman, and the Bahamas (*M. sagrae*), one on Jamaica and Hispaniola (*M. stolidus*), and one in the northern Lesser Antilles (*M. oberi*).

An attempt is made to reconstruct the evolution of these species as newly constituted, and to determine their relative ages, origins, and paths of entry into the West Indian region. It is postulated that *Myiarchus* entered the West Indies by four primary invasions: three by way of Jamaica, from the Honduran-Nicaraguan bulge, and one via Grenada from Venezuela. The oldest invasion, perhaps by an obscure species in the late Tertiary avifauna of Middle America, led to the development of *M. stolidus* on Jamaica and Hispaniola. Subsequent range expansions from Hispaniola led to the evolution of *M. sagrae* and *M. antillarum* in the

Greater Antilles and, more recently, to the polytypic *M. oberi* in the Lesser Antilles. In order not to obscure the relationships between these species, which are thought to have been derived from *stolidus* of Jamaica, it is recommended that they be considered a superspecies. After the submergence of the Greater Antillean land masses in the early Pleistocene, a second invasion of Jamaica by a Middle American *Myiarchus*, now obscure, resulted in the endemic *M. validus*. A third invasion of Jamaica, probably in the mid or late Pleistocene, by a representative of *M. tuberculifer* of Middle America, produced another endemic, *M. barbirostris*. The fourth invasion, no earlier than late Pleistocene, involved the range extension of *M. tyrannulus* from Venezuela into Grenada. With subsequent isolation this population evolved into *M. nugator*. Its expansion north of St. Vincent was blocked by a water barrier and competition with a congener already established on St. Lucia.

This study of insular populations supports evidence, gained previously from continental species of this genus, that suggests a relative plasticity of morphology in contrast to the conservativeness of certain vocal characters. It has also demonstrated the efficacy of using the behavioral responses of territorial males to experimental playback of vocal repertoires for determining the specific limits of allopatric populations of *Myiarchus*.

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