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Experiments on Species Discrimination in *Myiarchus* Flycatchers

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The many species of flycatchers belonging to the genus *Myiarchus* exhibit a remarkable uniformity in plumage color and pattern. This uniformity in morphology has led to considerable confusion and disagreement among taxonomists as to the specific limits within the group. Field workers have long been cognizant of rather pronounced differences in voice among these birds, and spectrographic analyses of the differences in audio characters have been evoked in recent revisions of certain complexes within the genus (Lanyon, 1960, 1961). That these conspicuous vocal differences function as the basis for species discrimination by these birds was the hypothesis tested in the series of field experiments reported on here.

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METHODS

Nineteen experiments were conducted in May, 1961, at the Kalbfleisch Field Research Station of the American Museum of Natural History, Huntington, New York. These involved a single pair of Great Crested Flycatchers (*Myiarchus crinitus*), the only representative of the genus in eastern North America. In this pilot study a single speaker, tape recording, and mounted specimen were used in each experiment to test the response

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of the territorial pair to a particular combination of audio and visual signals. Five standard playback tapes were used during these experiments, each representing the vocal repertoire of one of the five widespread species of *Myiarchus* of the North and Middle American mainland: Great Crested Flycatcher, Wied's Crested Flycatcher (*M. tyrannulus*), Ash-throated Flycatcher (*M. cinerascens*), Olivaceous Flycatcher (*M. tuberculifer*), and Nutting's Flycatcher (*M. nuttingi*). In the preparation of these tapes, an

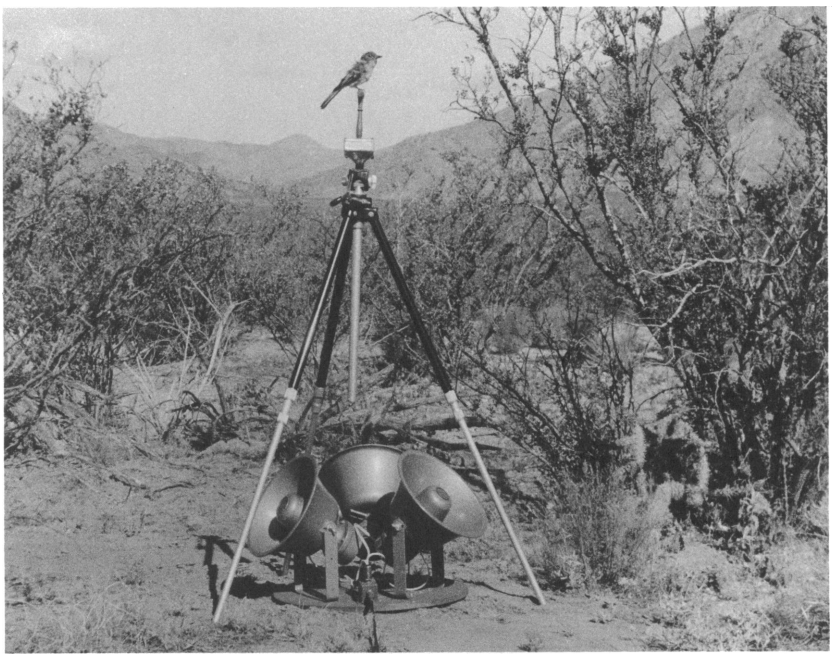

FIG. 1. Arrangement of speakers, tripod, and mount at an experimental location within a territory of *Myiarchus cinerascens*, near Portal, Arizona.

effort was made to make the vocal repertoires as complete as possible, including the most specifically characteristic vocal patterns used by each of these species during their territorial encounters. The original recordings were made during previous years' field work and in most cases included several widely separated geographical populations for each species. No appreciable geographical variation in vocalizations has been discovered in those members of the genus that have been intensively studied thus far (Lanyon, 1960, 1961). A Transmagnemite tape recorder, operating at 15 inches per second, and a one-watt, battery-powered amplifier and speaker were used for playback. A mounted bird was installed on a tripod

above the speaker to provide visual stimuli. The mounted specimens used were of *Myiarchus crinitus*, Tropical Kingbird (*Tyrannus melancholicus*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), Yellow-browed Tyrant (*Satrapa icterophrys*), Red-eyed Vireo (*Vireo olivaceus*), and Baltimore Oriole (*Icterus galbula*). The experiments varied in length from 10 to 40 minutes. A voice commentary of the progress of the experiment and of the positional and vocal response of the territorial birds to the experimental stimuli was recorded on an Executive tape recorder (1 7/8 inches per second) and later reproduced and analyzed in the laboratory. In addition, the response was further documented on 16-mm. film with a battery-powered Arriflex camera, with 200-mm. and 50-mm. lenses, and on 35-mm. film with a 400-mm. lens.

The results of these preliminary studies were of sufficient promise to warrant extension of this experimental approach, with some modifications, to other members of the genus. Three species of *Myiarchus* (*tyrannulus*, *cinerascens*, and *tuberculifer*) breed commonly and sympatrically in the vicinity of Portal, Cochise County, Arizona. From May 18 to May 29, 1962, 27 experiments were conducted in this area, with the base of operations at the Southwestern Research Station of the American Museum. Only the hours from 5 A.M. to 9.30 A.M. were used for experimentation. The Arizona experiments involved eight pairs of *M. tyrannulus*, seven pairs of *M. cinerascens*, and six pairs of *M. tuberculifer*. Most of these pairs were used for only a single experiment, and no pair was used for more than two. In those few instances in which a pair was involved in two experiments, there was a five- to seven-day interval between experiments.

The design of the Arizona experiments differed from that used in New York in that dual sets of auditory and visual stimuli were provided by the simultaneous playback of two distinct vocal repertoires and the use of two mounted specimens. A triangular arrangement of observer's position and two experimental positions was used. The two experimental positions were 75 feet apart, and at each of these locations there was a cluster of three speakers and a tripod supporting a mounted bird (fig. 1). The observer's position was situated at a point 50 feet from each of the experimental positions, and it was here that the recorders and cameras were operated (fig. 2). The location of each experiment was predetermined through observations of song perches, of territorial encounters, and (in two instances) of the nest cavities. Consideration was given to an uninhibited visibility from the observer's position and to the availability of perches within 6 feet of each of the experimental positions in the actual placement of mounted birds and speakers.

The speed of the two Transmagnemite recorders (15 inches per second)

was synchronized, so that all the playback tapes could be used interchangeably. Two 10-watt amplifiers, powered by rechargeable nickel-cadmium batteries, were operated adjacent to the recorders. A VU meter on each amplifier provided a monitor of the intensity of each output signal. Three Electrovoice speakers were used at each experimental position and were oriented to provide an omnidirectional dispersal of sound (fig. 1). The same five standard playback tapes used in New York

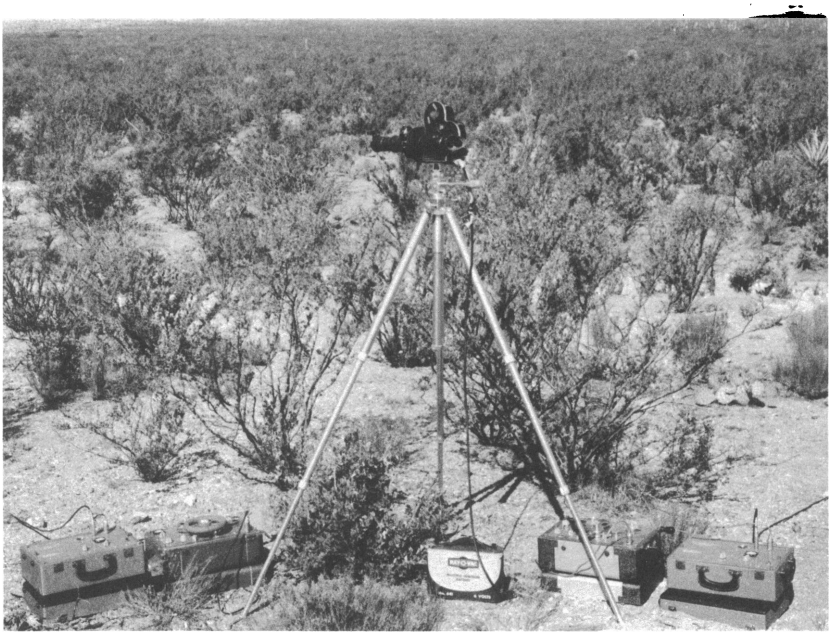

FIG. 2. Arrangement of tape recorders, amplifiers, and camera at the observer's position. Fifty-foot cables, at left and right, lead to the two experimental locations which are 75 feet apart.

(*crinitus*, *tyrannulus*, *cinerascens*, *tuberculifer*, *nuttingi*) were used in Arizona. The mounted birds in the Arizona experiments were of several species of *Myiarchus* (*M. tyrannulus magister*, *M. c. cinerascens*, *M. crinitus boreus*, *M. tuberculifer olivascens*, *M. n. nuttingi*, *M. validus*) and several "neutral" species (Hermit Thrush, *Hylocichla guttata;* Shrike-tanager, *Lanio fulvus;* and Dickcissel, *Spiza americana*).

Each Arizona experiment consisted of 16 minutes of playback of any two of the standard vocal repertoires, in combination with any two of the mounted specimens. After eight minutes of playback of the tapes, the

cables to the two speaker set-ups 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. The positions of the mounted birds were not altered during the course of an experiment. Each experiment thus provided two opportunities to observe orientation by territorial birds to one or the other of dual sets of audio and visual signals: an initial orientation at the commencement of playback,

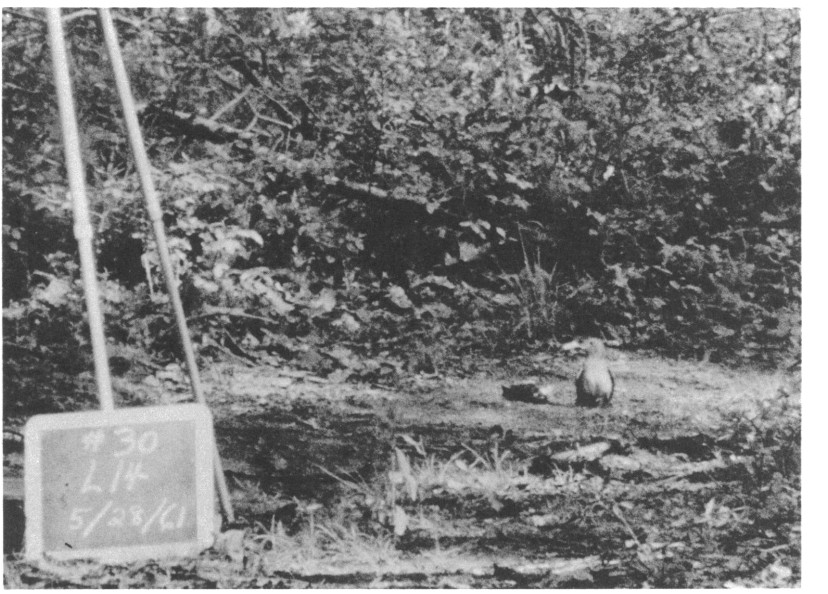

FIG. 3. One frame of a 16-mm. film of the experimental response of a male *Myiarchus crinitus* to a mount of a Yellow-bellied Flycatcher in association with a recording of *crinitus* vocalizations. Male has knocked the mount from the tripod (left) and continues its attack on the ground. A piece of the mount has been torn loose and appears in the bird's bill (experiment 30).

and a second orientation following the interchange of speaker cables. Orientation by the territorial birds to one of the experimental positions was interpreted as a positive response. For each positive response there was also recorded a corresponding negative response to the other set of audio and visual signals. Each positive response was classified according to one of three levels of intensity: (1) orientation to within 30 feet of a mount, involving frequent calling from perches in the immediate vicinity of the mount; (2) active criss-crossing of the experimental position, involving short flights over or about the mount and sometimes oriented

toward the mount itself ("passes"); (3) attacks on the mount, in which the territorial birds actually made contact with the mount. Each of the Arizona experiments was documented on film and tape as was done in the New York studies.

RESULTS

Eleven of the 19 experiments with *M. crinitus* involved the playback of the vocal repertoires of other species of *Myiarchus: tyrannulus*, four experiments; *cinerascens*, two experiments; *tuberculifer*, two experiments; and *nuttingi*, three experiments. The pair of *crinitus* did not respond positively in any of these 11 experiments, though a *crinitus* mount was used in all but two of them. Positive responses were observed in the other eight experiments in the series, and in all of these the playback tape used was that of the voice of *crinitus*. The mounts that were attacked, in association with *crinitus* voice, included a Kingbird, a Yellow-bellied Flycatcher (fig. 3), a Yellow-browed Tyrant, a Baltimore Oriole, and a Red-eyed Vireo.

The female of this pair of *crinitus* had been color-banded the previous year. Though both sexes oriented positively to the experimental area when *crinitus* tape was played back, only the unbanded male was involved in aggressive behavior directed toward the mounts.

The importance of species-specific audio signals in directing the territorial response of this pair of *crinitus* is illustrated in the following sequence of three experiments, all conducted on May 23, 1961:

EXPERIMENT 20, 9.30 A.M.: *Crinitus* tape with Kingbird mount (first use of this mount); immediate positive response, with many passes and attacks on the mount by the male; male still attacking when experiment was terminated at 10 A.M.

EXPERIMENT 21, 10.45 A.M.: When the pair next reached the experimental area in the course of their feeding movements, I played back *tyrannulus* tape with Kingbird mount; male was calling some 300 feet away, approached to within 50 feet, but not closer; eventually the pair left the area, with no positive response.

EXPERIMENT 22, 11.30 A.M.: *Crinitus* tape with Yellow-browed Tyrant mount (first use of this mount); responded immediately; during 30 minutes of playback, male made many passes at the mount; male knocked mount to the ground and continued to attack it there.

During the experiments with *crinitus* it became obvious that, once the pair had been attracted into the experimental area with playback of their own vocal repertoire, the intensity of the aggressive response to a particular mount increased with continued playback of their specific audio signals. The probability of an attack on a non-*Myiarchus* mount increased with time and with repeated exposure to the experimental conditions. The following series of three experiments on May 28, 1961, illustrates this

increase in responsiveness with continued playback of *crinitus* tape, and also reveals something of the minimum visual stimuli required as a focal point for the aggressive behavior of the male:

EXPERIMENT 31, 10.23 A.M.: *Crinitus* tape and Red-eyed Vireo mount (first use of this mount); pair oriented immediately; after six minutes of playback the male made a pass and attacked the mount viciously, dislodging the head, and flew to a perch with the head in his bill; male attacked body of the mount, knocking it to the ground; male attacked mount on the ground; terminated at 10.37 A.M.

FIG. 4. Experimental response of *Myiarchus tyrannulus* to a mount of *M. tuberculifer* in association with a recording of *tyrannulus* vocalizations (experiment 63).

EXPERIMENT 32, 10.45 A.M.: *Crinitus* tape and head of Red-eyed Vireo (from previous experiment) impaled on end of pointed stick; male continued criss-crossing the experimental area, making passes at the head; knocked head to the ground; terminated at 10.55 A.M.

EXPERIMENT 33, 10.58 A.M.: *Crinitus* tape; impaled some oak leaves on the end of the same stick used in previous experiment; male made one pass at the oak leaves; male studied the "mount" from nearby shrub, then hopped to the ground and oriented toward the speaker; remaining portion of 10-minute playback period spent on the ground in vicinity of speaker.

This increase in overt aggressiveness and lowering of the threshold of behavioral response to a particular set of visual signals, with continued playback of appropriate audio stimuli, could be the result of the birds'

becoming conditioned to or familiarized with the artificiality of the experiment. It might also be attributed to the cumulative effect of repeated stimulation by a particular mount in association with an appropriate vocal repertoire. More than likely both of these factors were operative. One consequence of these *crinitus* experiments was the standardization of the length of the subsequent experiments in Arizona, in order that I might better judge the relative stimulus value of the various mounts used.

The breeding territories of the three species of *Myiarchus* within the Arizona study area were frequently overlapping. Often two and sometimes all three species could be heard calling during the course of a single experiment. Whether or not a particular species oriented to one of the experimental positions depended on the audio signals used in playback. At no time did a male (or pair) respond positively unless its own vocal repertoire was being played back at one or the other of the two experimental positions. This disregard for the audio signals of congeneric species is well illustrated by experiments 47 and 48, which were conducted within a few minutes of each other, with the use of identical experimental positions:

EXPERIMENT 47: *Tuberculifer* tape and Dickcissel mount used at position A, and *cinerascens* tape and a *tuberculifer* mount at position B; all three *Myiarchus* species calling well prior to experiment; within two minutes after commencement of playback, a pair of *cinerascens* moved to within 30 feet of position B; noted that *tyrannulus* was calling well behind me, but not influenced by playback; after six minutes, one of the *cinerascens* had moved to within 4 feet of the mount at B, and a *tuberculifer* oriented to within 25 feet of position A; after seven minutes, one of the *cinerascens* made a pass at the B mount, and the *tuberculifer* was quite vocal within 15 feet of mount A; *tuberculifer* made a pass at A; switched the speaker cables; pair of *cinerascens* left position B and oriented toward position A, calling well within 8 feet of the mount; the *tuberculifer* left position A and perched within 10 feet of mount B; five minutes after the switch of cables, a *cinerascens* made a pass at the mount at A, and two more passes occurred during the ensuing three minutes; the *tuberculifer* made a pass at the mount at B and then perched 2 feet from the mount and called frequently; other member of the *tuberculifer* pair had appeared by this time; at conclusion of experiment, *tyrannulus* still calling well in general vicinity but not oriented toward either experimental position.

EXPERIMENT 48: Begun 10 minutes after completion of 47; *tyrannulus* tape and Dickcissel mount at position A, and *crinitus* tape and *tyrannulus* mount at position B; both *cinerascens* and *tuberculifer* continued to call periodically from the general area, but failed to orient toward either experimental position; within two minutes of playback, the pair of *tyrannulus* had oriented to position A, calling constantly; both members of the pair criss-crossed position A, keeping within a radius of 10 to 20 feet of the mount; no passes or attacks; following the switch of speaker cables, the pair of *tyrannulus* left position A and oriented toward position B, where they criss-crossed mount B, calling loudly; they remained in vicinity of B for 10 minutes following termination of experiment; no response from *cinerascens* or *tuberculifer*,

though these positions are within their defended territories, as evidenced by responses evoked in experiment 47.

When confronted with species-specific vocalizations at one position and the voice of a congener at the other position, the territorial birds invariably responded with characteristic aggressive behavior toward the mount that was "rendering" the species-specific audio signals. This response occurred without exception for 22 times in the case of *cinerascens*, for 20 times among *tyrannulus*, and for 18 times with *tuberculifer*. This positive response to their

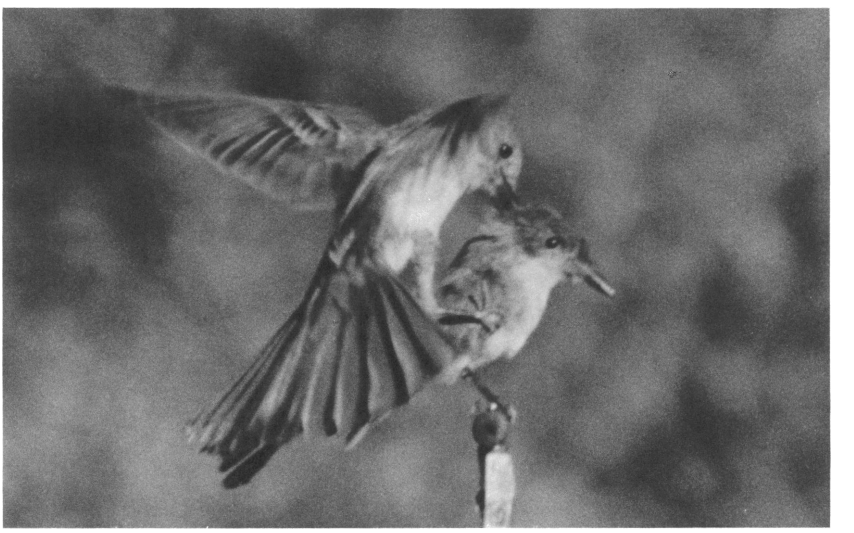

FIG. 5. Experimental response of *Myiarchus cinerascens* to a mount of *M. tuberculifer* in association with a recording of *cinerascens* vocalizations (experiment 51).

own specific voice and resulting negative response to the voices of congeners is summarized for all the experimental pairs in tables 1 to 3.

The failure of a territorial bird to respond to the voice of another species of *Myiarchus* was not improved by the association of the congeneric vocal repertoire with a mount of the species being tested. This was best revealed in those instances in which, after a switch of speaker cables, the experimental bird oriented away from a mount of its own species that had been "calling" conspecifically but that was now associated with a congeneric vocal repertoire. The experimental birds invariably abandoned this combination in favor of their species-specific vocalizations emanating from the other experimental position, though the mount there might be of another

TABLE 1

NUMBER OF RESPONSES OF *Myiarchus tyrannulus* TO COMBINATIONS OF RECORDINGS AND MOUNTS

(Eight pairs, 10 experiments, 20 opportunities for response.)

	Recordings of Another *Myiarchus*[a]			Recordings of *M. tyrannulus*		
	Neutral Mount	Mount of Another *Myiarchus*	Mount of *tyrannulus*	Neutral Mount[a]	Mount of Another *Myiarchus*[a]	Mount of *tyrannulus*
Negative response						
At start of experiment	4 (nu,cr3)	2 (nu,tu)	4 (cr,tu,ci2)	—	—	—
After interchange of cables	4 (ci,cr,nu,tu)	5 (ci,nu,tu,cr2)	1 (cr)	—	—	—
Positive response						
Oriented to within 30 ft. of mount	—	—	—	1 (di)	—	—
Passes and/or criss-crossing	—	—	—	6 (di3,ta3)	3 (cr,tu2)	1
Attacks on mount	—	—	—	1 (th)	4 (ci,cr,tu,va)	4

[a] Symbols in parentheses identify recordings or mounts as to species, and the figures in parentheses give the number of times used: ci, *cinerascens;* cr, *crinitus;* di, Dickcissel; nu, *nuttingi;* ta, Shrike-tanager; th, Hermit Thrush; tu, *tuberculifer;* va, *validus.*

TABLE 2

NUMBER OF RESPONSES OF *Myiarchus cinerascens* TO COMBINATIONS OF RECORDINGS AND MOUNTS

(Seven pairs, 11 experiments, 22 opportunities for response.)

	Recordings of Another *Myiarchus*[a]			Recordings of *M. cinerascens*		
	Neutral Mount	Mount of Another *Myiarchus*	Mount of *cinerascens*	Neutral Mount[a]	Mount of Another *Myiarchus*[a]	Mount of *cinerascens*
Negative response						
At start of experiment	4 (tu,ty,nu2)	4 (cr,nu,tu,ty)	3 (cr,nu,tu)	—	—	—
After interchange of cables	3 (tu,nu2)	3 (cr,tu2)	5 (cr,nu2,ty2)	—	—	—
Positive response						
Oriented to within 30 ft. of mount	—	—	—	3 (di3)	3 (cr,nu,tu)	3
Passes and/or criss-crossing	—	—	—	4 (di,th3)	3 (cr,tu,ty)	4
Attacks on mount	—	—	—	—	1 (tu)	1

[a] Symbols in parentheses identify recordings or mounts as to species, and the figures in parentheses give the number of times used: cr, *crinitus;* di, Dickcissel; nu, *nuttingi;* th, Hermit Thrush; tu, *tuberculifer;* ty, *tyrannulus.*

TABLE 3

NUMBER OF RESPONSES OF *Myiarchus tuberculifer* TO COMBINATIONS OF RECORDINGS AND MOUNTS

(Six pairs, nine experiments, 18 opportunities for response.)

	Recordings of Another *Myiarchus*[a]			Recordings of *M. tuberculifer*		
	Neutral Mount	Mount of Another *Myiarchus*	Mount of *tuberculifer*	Neutral Mount[a]	Mount of Another *Myiarchus*[a]	Mount of *tuberculifer*
Negative response						
At start of experiment	2 (ci2)	5 (ci,nu2,ty2)	2 (ci,cr)	—	—	—
After interchange of cables	3 (nu,ci2)	1 (cr)	5 (nu,ci2,ty2)	—	—	—
Positive response						
Oriented to within 30 ft. of mount	—	—	—	4 (th,di3)	5 (nu2,ci3)	4
Passes and/or criss-crossing	—	—	—	1 (di)	—	3
Attacks on mount	—	—	—	—	1 (nu)	—

[a] Symbols in parentheses identify recordings or mounts as to species, and the figures in parentheses give the number of times used: ci, *cinerascens;* cr, *crinitus;* di, Dickcissel; nu, *nuttingi;* th, Hermit Thrush; ty, *tyrannulus*.

species of *Myiarchus* or even a "neutral" species. Thus we see, for example, that on five occasions *cinerascens* oriented away from a mount of its own species, when that mount "changed" its voice from that of *cinerascens* to that of a congener as a result of the exchange of speaker cables (table 2).

Since I observed no positive response to the playback of any congeneric voice, there was no opportunity to determine the relative stimulus value of the voices of the various congeners. Special attention was given to the

FIG. 6. Experimental response of *Myiarchus tyrannulus* to a mount of a Hermit Thrush in association with a recording of *tyrannulus* vocalizations (experiment 63).

ability of *cinerascens* to discriminate between its own voice and that of *nuttingi*, a sibling species with which it is sympatric in parts of Mexico and with which it has been reported to hybridize (but see evidence against such hybridization in Lanyon, 1961). In all four of the experiments in which the voices of these siblings were played back simultaneously (providing eight opportunities for response), *cinerascens* oriented toward its species-specific repertoire and away from the voice of *nuttingi*. In four other experiments, staged in localities known to be actively defended by territorial *cinerascens*, the voice of *nuttingi* was played back in synchrony with a vocal repertoire other than that of *cinerascens*. There was no response from *cinerascens* in any of these instances. Likewise, special attention was given to the ability of *tyrannulus* to discriminate between its own voice and

the somewhat similar voice of an allopatric species, *crinitus*. In all four of the experiments in which the voices of these two species were used, *tyrannulus* oriented to its own vocalizations and away from the voice of *crinitus*. These results complement the negative response demonstrated by *crinitus* toward *tyrannulus* voice in the New York studies.

The intensity of a positive response by an experimental bird did not differ significantly according to whether its specific vocalizations were

FIG. 7. An attack by *Myiarchus tyrannulus* on a mount of a Shrike-tanager, provoked by repeated auditory stimulation with a recording of *tyrannulus* vocalizations. This response was not observed during the standardized experimental periods.

associated with a mount of its own species or with one of a congener. Expressed in different terms, the individuals tested did not discriminate between the visual signals presented by the various *Myiarchus* mounts used. All *Myiarchus* mounts seemed to be equally effective as a focal point for territorial aggression by a given species, providing they were "rendering" the voice of that species (figs. 4, 5). A *Myiarchus* mount had, however, more stimulus value than any of the neutral mounts used. Of the 11 occasions in the Arizona studies when a mount was actually attacked by an experimental bird, only one involved an attack on a neutral mount, that of a *tyrannulus* on a Hermit Thrush (fig. 6). With continued playback of their specific vocal repertoires beyond the experimental period, individuals of *cinerascens* and *tyrannulus* were stimulated to attack mounts of

several *Myiarchus* species and of a variety of "neutral" species, not indicated in tables 1 and 2. A *tyrannulus*, for example, attacked the black and fulvous plumaged Shrike-tanager after repeated auditory stimulation with *tyrannulus* playback (fig. 7).

If one compares the positive responses of the three Arizona species, there appears to be some correlation between body size and relative intensity of response. The largest of the three, *M. tyrannulus*, was definitely the most

FIG. 8. An attack by *Myiarchus cinerascens* on a mount of *M. crinitus*, provoked by repeated auditory stimulation with a recording of *cinerascens* vocalizations. This response was not observed during the standardized experimental periods.

aggressive, as evidenced by the greater number of attacks during the standardized experimental periods. The smallest species, *M. tuberculifer*, was the least aggressive. Only one attack by this species occurred during the experiments (on a mount of *nuttingi*), and none could be provoked by continuation of playback as was done for purposes of photographic documentation in both *tyrannulus* (fig. 7) and *cinerascens* (fig. 8).

SUMMARY

1. Field experiments were conducted on one species in New York

(*Myiarchus crinitus*) and three species in Arizona (*M. tyrannulus*, *M. cinerascens*, *M. tuberculifer*) to test the hypothesis that differences in vocalizations function as the basis for species discrimination by these birds.

2. The response of territorial birds to various combinations of audio signals afforded by playback of prepared tapes of five species of *Myiarchus*, and to visual signals provided by mounted specimens of *Myiarchus* and non-*Myiarchus* species, was observed and photographed.

3. Each of the four species demonstrated an ability to discriminate between the vocal repertoires of five species of *Myiarchus* and reacted positively only to that repertoire representative of its own species.

4. Each of the four species reacted aggressively and even attacked mounted specimens, irrespective of species, providing these specimens were associated experimentally with playback of the vocal repertoire characteristic of the species being tested.

5. There was no evidence of discrimination by experimental birds between the visual signals presented by the various *Myiarchus* mounts used, but *Myiarchus* mounts appeared to have more stimulus value than mounts of non-*Myiarchus* species.

6. These results support the hypothesis that differences in vocalizations do function as the basis for species discrimination by these birds. They also lend weight to the use of species-specific vocal patterns as legitimate taxonomic characters, when considered in conjunction with more conventional morphological characters, in the establishment of specific limits and relationships within this difficult genus.

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