

EXPERIMENTS ON SPECIES DISCRIMINATION IN BLUE-WINGED WARBLERS

FRANK B. GILL AND WESLEY E. LANYON

DISCRIMINATION of species by birds may be dependent upon appropriate visual and auditory stimuli. Lack's study (1943) of the Robin (*Erithacus rubecula*) demonstrated the importance of a visual stimulus, the red breast. Other more recent studies (Dilger, 1956; Stein, 1958, 1963; Lanyon, 1963) have demonstrated the lack of importance of morphology and the reliance on auditory signals in certain species. Wood warblers (Parulidae) possess complex species-specific plumage patterns and vocalizations and might therefore rely on both types of stimuli. Species discrimination within the Blue-winged Warbler (*Vermivora pinus*) and Golden-winged Warbler (*V. chrysoptera*) complex is of particular interest because of the frequent hybridization of these birds in some areas of sympatry (Carter, 1944; Parkes, 1951; Berger, 1958; Short, 1963).

The experiments discussed in this paper were designed to determine the basis for species discrimination in a population of Blue-winged Warblers on Long Island, New York, an area in which the Golden-winged Warbler is rarely found breeding. Morphologically, specimens from this population exhibit little evidence of introgression (Short, 1963).

METHODS

Preliminary experiments, in which visual and auditory stimuli were tested simultaneously, were conducted during the first two weeks of June, 1961. Data from these experiments were used to establish procedures followed in 1962 and 1963.

A series of 22 experiments, testing the responses of 11 males (8 color-banded) to visual stimuli, was conducted 7-11 June 1962. The location used for each experiment in this series (and in all subsequent series) was within the defended territory of a male, close to a frequented singing perch or, when possible, near the nest. No male was tested more than three times, with a minimum of 36 hours between successive experiments. In each experiment, one mounted bird was attached to the top of a tripod. In addition to a male *V. pinus* and a male *V. chrysoptera* the following mounts were used: a Tennessee Warbler (*V. peregrina*) of plain gray-green plumage, a female Yellow Warbler (*Dendroica petechia*) of dull yellow plumage, and a male Chestnut-sided Warbler (*D. pensylvanica*) with conspicuous markings and a yellow crown. The male was attracted to the vicinity of the mount by a recording of the *pinus* vocalization phoneticized as *bee buzzz* (Figure 1, A). This vocalization was provided

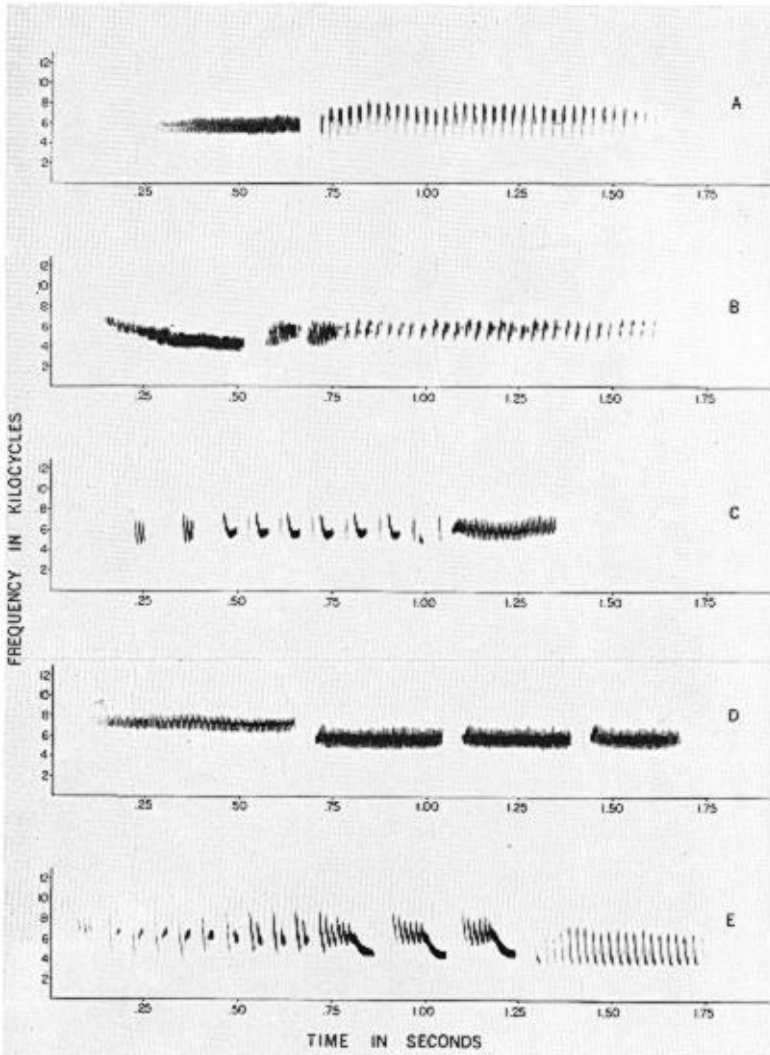


Figure 1. Sound spectrograms of the vocalizations of Blue-winged and Golden-winged warblers used in playback experiments (top to bottom): A, *Vermivora pinus*, song type I; B, *V. pinus*, song type I; C, *V. pinus*, song type II; D, *V. chrysoptera*, song type I; E, *V. chrysoptera*, song type II.

by a Transmagnemite tape recorder operated at a distance of 16 meters from the mount. Amplification was provided by a 10 watt amplifier operated adjacent to the recorder. A VU meter on the amplifier provided a monitor of the intensity of the output signal. The recording was played through a unit of three Electrovoice speakers under the tripod bearing

the mount. Playback was terminated when the bird was within three meters of the mount. The response during the 30 minutes following the initial termination of playback was then evaluated. If the bird left the experimental area before the end of the 30 minutes, it was re-attracted by the playback.

Two distinctive vocalizations are characteristically associated with territorial behavior in Blue-winged Warblers. We have arbitrarily designated these as song type I (Figure 1, A, B) and song type II (Figure 1, C) for lack of information concerning their functional significance. Golden-winged Warblers have two comparable song types, which have been similarly designated (Figure 1, D, E). The considerable variability in the composition of song type I within the Long Island population of Blue-winged Warblers (Lanyon and Gill, MS) prompted us to use two variations of this vocalization (Figure 1, A, B) in our playback experiments. Since there was no apparent differential response to these variations, we include them under the single designation "song type I."

A second series of 22 experiments, testing the responses to auditory stimuli, was conducted on 13 and 14 June 1962. Of the 11 males tested in the previous series, 8 were used. Two of the males were tested in two experiments each, while each of the other 6 was tested in three experiments. An experiment consisted of the simultaneous playback of two of the following six recordings of vocalizations commonly used by territorial males of five parulid species: *Vermivora pinus* (song type I and II), *V. chrysoptera* (song type I), Black-throated Green Warbler (*Dendroica virens*), *D. pensylvanica*, and *D. petechia*. The *V. pinus* recordings were made at the Kalbfleisch Field Station. All other recordings were copied from Cornell University phonograph records: *V. chrysoptera*, *D. petechia*, and *D. pensylvanica* (Kellogg and Allen, 1959); *D. virens* (Kellogg and Allen, 1953). Each of the two speaker units, placed 23 meters apart, consisted of three speakers oriented to provide an omnidirectional dispersal of sound. Two identical recorders and amplifiers (specified above) were operated at a location 16 meters from either speaker. The speeds of the two recorders (15 inches per second) were synchronized so that all of the playback tapes could be used interchangeably. The experiments averaged 12 minutes in length. At the midpoint of each experiment the speaker cables were interchanged, thus effecting an exchange of positions of the respective playbacks for the duration of the experiment. Each experiment, therefore, provided two opportunities for orientation by a territorial male, an initial orientation at the commencement of dual playback, and a second orientation following the interchange of speaker cables.

A series of 8 experiments, conducted 4-6 June 1963, tested the responses of 8 color-banded males to auditory stimuli and completed the studies of

the Long Island population. None of these males had been tested in previous years. All of the experiments in this series consisted of the simultaneous playback of two recordings: *V. pinus* song type II, and *V. chrysoptera* song type II (the latter recorded in Rockland County, New York). The experimental procedure was the same as that used in the 1962 dual playback experiments.

RESULTS

RESPONSES TO VISUAL STIMULI (TABLES 1 AND 2)

The experimental responses to visual stimuli were evaluated on the basis of the following criteria.

Active Behavior.—This is characterized by the bird flitting around the experimental area, often to opposite sides of the mount. The short flights included a vertical tail-pumping, suggestive of the behavior of a Yellowthroat (*Geothlypis trichas*), and also a spreading of the tail, briefly exposing the white patches. While perched, the bird would flick (i.e., rapidly

TABLE 1
SUMMARY OF EXPERIMENTS TESTING VISUAL DISCRIMINATION

Male	Breeding status	Sequence of experiments	Mount used	Type of response pattern
Number 1	Nest with young 150 feet from experimental site.	I	<i>V. chrysoptera</i>	3
		II	<i>V. pinus</i>	1
Number 2	Paired, but nest not found.	I	<i>V. pinus</i>	1
		II	<i>V. chrysoptera</i>	*
		III	<i>V. peregrina</i>	1
Number 3	Male carrying food on 14 June.	I	<i>V. pinus</i>	1
Number 4	Nest with young 50 feet from experimental site. Young fledged just prior to exposure III.	I	<i>V. pinus</i>	1
		II	<i>V. peregrina</i>	3
		III	<i>V. pinus</i>	1
Number 5	Paired?	I	<i>V. pinus</i>	1
		II	<i>V. peregrina</i>	3
		III	<i>D. petechia</i>	1
Number 6	Nest with young 50 feet from experimental site.	I	<i>V. pinus</i>	2
		II	<i>V. chrysoptera</i>	2
Number 7	Nest with young 50 feet from experimental site.	I	<i>V. pinus</i>	1
		II	<i>D. petechia</i>	3
Number 8	Nest with eggs 300 feet from experimental site.	I	<i>V. pinus</i>	1
		II	<i>V. chrysoptera</i>	3
Number 9	Nest with young 75 feet from experimental site.	I	<i>V. pinus</i>	1
		II	<i>D. pennsylvanica</i>	3
Number 10	Paired.	I	<i>V. chrysoptera</i>	3
		II	<i>V. chrysoptera</i>	2
Number 11	Nest with young 60 feet from experimental site.	I	<i>D. petechia</i>	3

* Eliminated due to faulty experimental procedure.

TABLE 2
ANALYSIS OF RESPONSES TO VISUAL STIMULI

Mount	Number and strength of responses			Total experiments	Ratio of responses with Waning to total number of responses to mount	Ratio of responses with attacks to total number of responses to mount
	Exposure 1	Exposure 2	Exposure 3			
<i>V. pinus</i>	7 strong 1 weak to strong	1 strong	1 strong	10	1/10	5/10
<i>V. chrysoptera</i>	2 weak	1 weak 2 weak to strong	—	5	5/5	3/5
<i>D. petechia</i>	1 weak	1 weak	1 strong	3	2/3	1/3
<i>V. peregrina</i>	—	2 weak	1 strong	3	3/3	1/3
<i>D. pensylvanica</i>	—	1 weak	—	1	1/1	0/1

open and close) its wings and tail simultaneously. Chips were the normal vocalization associated with this behavior.

Study Behavior.—The responding bird would sit almost motionless on a perch within three meters of the mount, usually silent or with occasional low-intensity vocalizations (song type II and twittering). Preening, stretching, bill-wiping, and fluffing of the flank feathers were associated with this behavior. Prolonged Study Behaviors up to 30 minutes were not uncommon.

Pass.—A flight directed towards the mount but not resulting in actual contact.

Attack.—Here contact either brief or sustained, was made with the mount. The attacking male usually landed on the back of the mount and pecked at the crown (Figure 2).

Wane.—This term represents a movement away from the experimental area, with resumption of full-intensity vocalizations and territorial activities.

Both Active and Study Behavior were indicative of a strong response, as revealed by their frequent association with Attacks, Passes, and long, continued responses. Waning, on the other hand, was considered a weak response to the mount, a contention which was supported by the regular occurrence of Waning following the removal of all mounts.

These components of experimental responses are similar to behavior we have observed in natural territorial encounters. Active Behavior is the basic feature of intense or prolonged encounters, the short flights frequently supplanting the rival male. Most encounters, usually brief, result in the established male chasing the rival several hundred yards, well out



Figure 2. Male Blue-winged Warbler attacking *Vermivora pinus* mount.

of the territory. Actual contact between two birds is infrequent, though occasionally two males do meet in mid-air and fall together to the ground. Vocalizations other than chips are rare in actual encounters but are usually given afterwards. The major difference between natural and experimentally-evoked responses is the common occurrence of Study Behavior in the latter. This is undoubtedly a consequence of the artificiality of the experimental conditions.

Three patterns of experimental responses, based upon the behavioral criteria discussed above, were evident.

Response Pattern 1.—This is a strong, continued response, which was considered to be a reflection of a strong stimulus value of the mount. Eleven experiments involved this response pattern. Interruptions, caused by natural territorial encounters or unknown factors, but which were followed by a return to the experimental area without re-attraction by playback, did not negate the continuity of the response. Example from field notes: Experiment 76 using a *V. pinus* mount and testing male 4 for the first time.

After one-half minute of playback, male responded with Active Behavior, tail-pumping and flicking, and bill-wiping on perches, approaching to 30 feet. After four minutes, it changed to Study Behavior 15 feet from mount. Relocations of study perches accompanied by tail-pumping brought the bird to four feet after 16.5 minutes.

Study Behavior continued for the duration of the experiment. After 30 minutes the mount was removed, and the male retreated 40 feet, returned to 25 feet, but then dropped to 60 feet and started giving song type I. During the following 10 minutes it moved off several hundred feet, singing song type I.

Response Pattern 2.—This involves initial Waning(s), necessitating re-attraction but terminating in a strong response including an Attack. Only three experiments involved this response pattern. The terminal strong response appears to contradict the meaning of the initial Waning. However, two of the three experiments involving this response pattern included natural territorial encounters which thus conflicted with the experimental stimuli and could have been responsible for the initial unresponsiveness. Previous experience might also have been a factor since two of the three experiments involved second exposures for the birds concerned, and one of these exposures followed a pattern 3 response by the same bird to the same mount. Example from field notes: Experiment 79, testing male 6 for the first time and using a *V. pinus* mount:

Initial playback attracted male to general area. Tape rewound and playback restarted with male in general area. Approached mount but then changed into a Study Behavior for five minutes 25 feet from mount. It then wandered away and playback was restarted. It responded but almost immediately chased a second blue-wing out of the territory. Playback consequently stopped and restarted two minutes later. It responded with Active Behavior, silent, passed at the mount several times and then attacked two minutes after the final termination of the playback. Following removal of mount, it preened for several minutes on a perch five feet from tripod and then moved off giving song type I.

Response Pattern 3.—This is an immediate strong response, but one terminating in a weak response and Waning. Eight experiments involved this response pattern. This response reflects a lack of stimulus value of the mount and an ability of the territorial male to discriminate visually. An immediate strong response of brief duration is to be expected as the result of the auditory stimulation and was noted in all of the 1962 experiments. Response pattern 3 was not considered significant unless it was preceded or followed by an experiment evoking a strong response. Example from field notes: Experiment 82 using a *V. peregrina* mount and testing male 4 for the second time:

Male 4 responded after one-half minute of playback, carrying food, in Active Behavior. Playback terminated after three minutes with male 10 feet from mount. After one minute it dropped back to 30 feet, singing song type I, and then moved to several hundred feet from mount.

Playback was begun again when male was several hundred feet from mount, four minutes after the original termination. Male responded almost immediately, approaching to 8 feet. Playback stopped after two minutes. Brief period of Active Behavior followed by movement to far side of the territory and resumption of full intensity

song type I. Nine minutes later male approached the mount to 25 feet, feeding and singing and then dropped back to 50 feet.

Fourteen minutes after second termination, playback was restarted for two minutes with male in general area. It responded almost immediately with Active Behavior, then into Study Behavior 10 feet from mount, giving weak song type I. After one and one-half minutes male changed to Active Behavior, with feeding and occasional twitterings. Then it reapproached the mount to 1 foot and left the experimental area.

Two experiments placed in this category differed from the others in that the response after playback was abnormally intense or long. Both were second exposures of the males to the experimental conditions. The initial strong responses were followed by a typical Wane, thus indicating a low stimulus value of the mount.

Notes.—The fact that only *V. pinus* mounts consistently evoked strong, continued responses (see Table 2), and the contrasts in the behavior of individual males to *pinus* and “non-*pinus*” mounts in successive experiments, demonstrate that the male Blue-winged Warblers discriminated visually between some of the mounted birds.

The actual role of the visual stimuli could apparently be influenced by other factors. For example, the attraction of the males into the experimental area by the playback of sound recording is indicative of the influence of auditory stimuli. Exposure to previous experimentation is also important, as was illustrated by the increase in the strength of the responses evoked by “non-*pinus*” mounts in the sequence of experiments with individual males. All three first exposures using these mounts resulted in weak responses. Of the 7 responses to second exposures, 5 were weak and 2 were slightly stronger (pattern 2). Both of the third exposures resulted in strong continued responses. The combined effect of these factors was such that any of the mounted birds was subject to attack. Supporting this contention is the fact that attacks were involved in 5 of the 12 responses to “non-*pinus*” mounts.

Finally, neither the phase of the nesting cycle nor the location of the experimental setup with respect to an active nest appeared to have a consistent effect upon the responsiveness of a territorial male. Females did not respond to any of our experiments.

RESPONSES TO AUDITORY STIMULI

The experimental responses to auditory stimulation were evaluated as follows. The failure of a territorial male to respond to playback indicated a lack of stimulus value of both recordings used. Attraction to the general area and a continued response, but lack of orientation toward a particular speaker location, indicated an equivalent stimulus value of the two recordings. Orientation toward a particular recording indicated a com-

paratively stronger stimulus value of that recording and an ability of the male to discriminate between the two sets of auditory stimuli. A continued response to a given recording, effected by the reorientation of the male following the interchange of cables, provided confirmation of the greater stimulus value of that particular vocalization. If a recording failed to evoke a strong response after a shift in location, the relatively great strength of the stimulus value of that recording, indicated by the initial orientation, was negated.

Of the 22 dual playback experiments conducted in 1962, 9 tested a combination of *V. pinus* and "non-*pinus*" vocalizations. In 8 of these, of which 5 involved *V. chrysoptera* song type I, the male responded strongly to *pinus* during both the initial orientation and the reorientation. In the ninth experiment, a combination of *V. pinus* and *V. chrysoptera* vocalizations, the male responded predominately to the *pinus* playback although there was a delay of three minutes following the interchange of speaker cables before he reoriented to the new *pinus* location.

Five experiments combined *chrysoptera* song type I with a "non-*Vermivora*" vocalization. The responses to these were weak and varied. In the one *V. chrysoptera/Dendroica virens* experiment, the male remained essentially midway between the two speakers. In the two other experiments with this male, however, *pinus* playback evoked a strong response when combined both with the *V. chrysoptera* and *D. pensylvanica* recordings. In one of the two experiments combining the *V. chrysoptera* and *D. petechia* recordings, the male did not respond at all. This experiment was followed immediately by another in which a *pinus* playback did evoke a strong response. In the other *V. chrysoptera/D. petechia* experiment, the male oriented to the *petechia* recording for the first three minutes but then moved to a point midway between the speakers, failed to reorient after the interchange, and then left the experimental area. Two experiments combined the *V. chrysoptera* and *D. pensylvanica* recordings. There was no response in one of these, although the same male responded strongly to *pinus* playback in a subsequent experiment. In the other experiment with this combination the male oriented toward the *chrysoptera* recording but with a less intense response than that evoked by *pinus* playback.

The remaining eight dual playback experiments consisted of combinations of two *pinus* vocalizations and resulted in strong responses in all cases. Additional data are needed before the relative stimulus value of each of these *pinus* vocalizations can be ascertained.

The 8 dual playback experiments conducted in 1963 tested the ability of 8 males to discriminate between *pinus* song type II and *chrysoptera* song type II. Only 1 male gave a strong consistent response exclusively to the *pinus* vocalization. Three males were attracted to the experimental

area but exhibited no consistent orientation, often remaining midway between the two speakers. The remaining 4 males responded strongly to both playback vocalizations, with frequent reorientations to the two speakers.

In summary, these experimental responses to auditory stimuli clearly indicate that male Blue-winged Warblers in the Long Island population do discriminate acoustically. *Pinus* vocalizations consistently attracted and excited a male whereas "non-*pinus*" vocalizations, with the exception of *chrysoptera* song type II, evoked only weak responses or none at all. When given the opportunity, most of the males tested failed to discriminate between *pinus* song type II and *chrysoptera* song type II.

DISCUSSION

Our experiments on Long Island suggest that male Blue-winged Warblers in a nearly "pure" population are able to discriminate visually between mounted specimens of *V. pinus* and *V. chrysoptera*. These warblers are also able to discriminate between some of the characteristic vocalizations of the two species (song type I) but not between others (song type II). Little is known, however, of the territorial interrelationships of *pinus* and *chrysoptera* on a common breeding ground. It is not clear, for example, to what extent *pinus* and *chrysoptera* defend overlapping or mutually exclusive territories in areas of sympatry. Responsiveness of male *pinus* and *chrysoptera* to each other (i.e., a failure to discriminate visually and acoustically) would result in the maintenance of mutually exclusive territories. On the other hand, discrimination, such as was exhibited by Long Island *pinus*, would probably result in the maintenance of overlapping territories.

Some insight into the behavior of sympatric birds was obtained from a preliminary series of 9 dual playback experiments that we conducted on 3 June 1963 at one location in Rockland County, New York. In this series, a single male *pinus* and a single male *chrysoptera* were tested. Both of these males, which were taken as specimens, showed evidence of introgression in their wing bars, but otherwise were typical of their respective species in plumage and voice. The recordings and procedure used did not differ from the Long Island dual playback experiments. Strong responses were evoked simultaneously from both males at a single experimental location, but only to their respective song type I's. In addition, neither male responded to the song type I of the other species when this vocalization was tested in combination with a *Dendroica pensylvanica* recording. This discrimination with respect to song type I was similar to that exhibited by Long Island *pinus*, and suggests that these males were, indeed, maintaining overlapping territories. Unlike most of the Long Island *pinus*,

the two individuals in Rockland County also discriminated between their song type II's when these two vocalizations were presented simultaneously in a dual playback experiment. Although the results of these experiments are admittedly fragmentary and inconclusive with respect to the behavior of these warblers in areas of sympatry, they do provide argument against the view that there is a complete breakdown of species discrimination by males in such areas.

Unlike the situation on Long Island, where males are responding to essentially "pure" auditory and visual stimuli, the problem of species discrimination in areas of sympatry is complicated by the presence of intermediate plumage types, aberrant or intermediate vocalizations, and individuals with the plumage of one species and the vocal repertoire of the other. This resulting gradient of visual and auditory stimuli could conceivably alter the discriminatory behavior of the breeding males of such a population. It was apparent from our Long Island studies that the discriminatory behavior of male *pinus* could be altered by exposure to *chrysoptera* stimuli in combination with highly stimulating *pinus* vocalizations and mounts. For example, we have seen that the role of visual discrimination in evoking territorial aggression can be influenced by other factors; any parulid mount was subject to attack when associated with a highly stimulatory vocalization. The 5 attacks in 12 experiments with "non-*pinus*" mounts associated with *pinus* vocalizations bear this out. That the stimulus value of a particular vocalization relative to that of a *pinus* vocalization can also be modified was illustrated by the preliminary experiments in 1961 in which three males eventually responded strongly to the *chrysoptera* song type I recording. This occurred only after repeated exposure to the experimental conditions which associated the *chrysoptera* recording with highly stimulating *pinus* vocalizations and mounts.

Finally, it should be remembered that the results discussed in this paper deal exclusively with the discriminatory behavior of territorial males. They cannot, therefore, be interpreted as necessarily having a bearing on the stimuli involved in pair formation and the ultimate problem of reproductive isolation, or lack thereof, in this complex.

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SUMMARY

Field experiments testing the discriminatory behavior of territorial male Blue-winged Warblers (*Vermivora pinus*) in a population where no Golden-winged Warblers (*V. chrysoptera*) occurred revealed that: (1) both visual and auditory stimuli were important; (2) the plumage and song type I of *chrysoptera* were relatively less effective than were the plumage and song type I of *pinus*; (3) song type II of *pinus* was not distinguished from song type II of *chrysoptera*; (4) the discriminatory behavior of male *pinus* can be altered with experience. In preliminary experiments that tested a male *pinus* and a male *chrysoptera* on a common breeding ground, the males discriminated between auditory stimuli, including their respective type II songs, suggesting that they were holding overlapping rather than mutually exclusive territories.

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The University of Michigan Museum of Zoology, Ann Arbor, Michigan, and The American Museum of Natural History, New York 24, New York.