AMERICAN MUSEUM
Novitates

PUBLISHED BY
THE AMERICAN MUSEUM
OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2666 JANUARY 9, 1979

WESLEY E. LANYON

Development of Song in the Wood Thrush (*Hylocichla mustelina*), With Notes on a Technique for Hand-rearing Passerines from the Egg

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024

Number 2666, pp. 1-27, figures 1-10, tables 1-5 January 9, 1979

Development of Song in the Wood Thrush (*Hylocichla mustelina*), With Notes on a Technique for Hand-Rearing Passerines From the Egg

WESLEY E. LANYON[1]

ABSTRACT

Two Wood Thrushes (*Hylocichla mustelina*), reared from the egg in isolation from experienced conspecifics, developed song that is remarkably species-specific, but lacking in certain characteristics of the central phrases. Wild Wood Thrushes failed to respond to the playback of the isolates' songs, which suggests that features of the central phrase, normally learned from experienced conspecifics during the first 10 months of age, may transmit information required for species-recognition in this species. An unusually detailed account updates the author's technique for hand-rearing passerines from the egg, including simplification of equipment and diet.

INTRODUCTION

The evidence from recent experimental research and a reappraisal of earlier, less sophisticated studies, suggests that learning from experienced conspecifics plays a significant role in the development of normal primary song in many species of passerine birds. Experimental isolates deprived of such a learning experience develop song that is at least qualitatively different from that of their wild counterparts (for reviews see Lanyon, 1960; Marler, 1964; Konishi and Nottebohm, 1969; Nottebohm, 1970, 1975; and Marler, 1977). The number of passerines for which we have data is still small, however.

Differences in experimental design and in the analytical procedures used to examine "normalcy" have led to discrepancies in the literature as to the abilities of isolates to develop songs characteristic of their species. Although it has been generally assumed, for example, that isolation of nestlings is as effective experimentally as isolation from the egg stage, it is unwise to rule out the possible role of learning during the prenatal period. The embryos of some precocial birds are capable of audition and of vocalization several days before hatching, and are responsive to the maternal and sibling calls of their own species (Gottlieb, 1968; Gottlieb and Vandenbergh, 1968; Vince, 1969). In a pioneering study that stimulated additional research in laboratories around the world, Messmer and Messmer (1956) reported that European Blackbirds (*Turdus merula*), reared from the egg in isolation from experienced birds, are able to develop "normal" species-specific songs. But when these so-called

[1]Chairman and Lamont Curator of Birds, Department of Ornithology, the American Museum of Natural History.

ISSN 0003-0082 Price $2.10

normal songs of the isolates were subsequently analyzed spectrographically, they were found to differ from songs of wild blackbirds in a number of subtle characteristics (Thielcke-Poltz and Thielcke, 1960). Furthermore, there are spectrographic differences between the songs of the egg-isolates of the Messmers' and the songs of the nestling-isolates studied by Thielcke-Poltz and Thielcke, but it is unclear whether such differences can be attributed to individual variation or to the differences in auditory experience (Konishi and Nottebohm, 1969).

Clearly, the prudent procedure in studies of the development of avian vocalizations would be to hand-rear the experimental isolates from the egg whenever possible. Unfortunately, the problems associated with hand-rearing the altricial young of passerines have been so formidable as to force most investigators to use "isolates" obtained as nestlings or to use foster parents (usually canaries) to hatch the eggs and rear the young.

In the study of song development reported on here, two Wood Thrushes (*Hylocichla mustelina*) were hand-reared from the egg-stage and isolated from experienced birds for nearly two years. The study was designed to determine if (1) the Wood Thrush isolates would develop a normal, species-characteristic primary song under these conditions of isolation, and if (2) after exposure to an enriched auditory environment, including the frequent singing of a wild Wood Thrush on territory, the two-year-old experimental birds would add to or modify their isolate-song. The "normalcy" of isolate song is judged through (1) spectrographic comparison with the songs of wild birds and by (2) the responses of wild birds in playback experiments using songs of both isolates and wild birds. The only previously published data on the development of song in experimentally isolated thrushes, family Turdidae, are those on the European Blackbird cited above.

At the time of my review of this field in 1960, I knew of only four species of passerines that had been studied in isolation from the egg-stage. To my knowledge no laboratory other than my own has made any significant progress in this technology since then. My technique for hand-rearing passerines from the egg has been much simplified and made more effective since earlier reports (Lanyon and Lanyon, 1969, 1971). The changes in equipment and procedure have been considerable, and judging from correspondence, there is a continuing demand by investigators for such information. The unusually detailed account of the experimental technique used to hand-rear the Wood Thrushes in this study will serve to update this technique.

ACKNOWLEDGMENTS

I am indebted to the Long Island Park Commission for permission to study Wood Thrushes at the Connetquot River State Park, where my fieldwork was greatly facilitated by the generous assistance and cooperation of Mr. Gilbert Bergen and staff. Mr. James Mansky, Resident Superintendent, of the Kalbfleisch Field Research Station of the American Museum of Natural History shared in the responsibility for maintenance of the isolates and made some of the recordings of their songs. I am particularly grateful to my wife, Vicky, who helped to develop the technique for hand-rearing songbirds from the egg, shared in the responsibility of rearing and caring for the experimental Wood Thrushes, and assisted in conducting the playback experiments, and in the spectrographic analysis of the songs. Financial support came principally from the Kalbfleisch Endowment Fund of the American Museum of Natural History.

METHODS

Analysis of the Song of Wild Birds

The song repertoires of seven wild Wood Thrushes were recorded and analyzed spectrographically to provide a basis for an analysis of the performance of the isolates. None of these wild birds was color-banded, but each could be identified individually by its distinctive and unique repertoire of song patterns. Two of these birds were recorded at the American Museum of Natural History's Kalbfleisch Field Research Station in Huntington, Suffolk County, New York, where the usual complement of territorial pairs is two. The remaining five were recorded at the Connetquot River

State Park in Islip, New York, a straight-line distance of 17 km. SE of the Kalbfleisch Station on Long Island. All recordings were made monaurally on a Uher 4400 Report Stereo, operating at 19 cm. per second, using a Uher microphone, model M517, mounted at the focal point of a 61 cm. fiber glass parabolic reflector. A Uher microphone gain amplifier, 106GA, was used to provide additional signal amplification as needed. Whenever a new recording was made, the tone of a pitch pipe (middle "A," 440 Hz.) was recorded as a permanent and convenient check on the speed of the recorder at that instant and to check for possible distortion. The sample sizes (number of song renditions in each song bout) for these seven birds is indicated in table 1.

These samples were analyzed with a Kay Elemetrics' audio spectrum analyzer, Sona-Graph Model 6061B. The resulting sound spectrograms graphically portray frequency (kHz. = kiloHertz = kilocycles per second) against time (seconds). I used the flat response setting (FL-1) and the linear frequency scale. A frequency scale of 0.16 to 16 kHz. was required due to the presence of fundamental signals above 8 kHz. (the scale normally used). Consequently, the wide-band filter, used for increased resolution in time, was 600 Hz. in width. All displays are reproduced here as half-tone illustrations, thus preserving the maximum detail possible.

The Experimental Birds

A complete clutch of three eggs was taken from a Wood Thrush nest located at the Kalbfleisch Field Research Station on June 29, 1974. The eggs were candled, estimated to have been incubated for five to six days, and placed in an isolation chamber (adapted to serve as a still-air incubator) in one of the Station's laboratories. Two eggs hatched on July 6, after seven days of artificial incubation. When I examined the third egg on July 8, I found that the embryo had died, apparently just prior to pipping.

The two experimental Wood Thrushes fledged at 12 days of age but were retained in the isolation chamber until they were feeding for themselves at three weeks of age. At that point they were transferred to a "white-noise room" at the Station, where they were held for nearly two years, in continued isolation from all other birds. They were color-banded and hereinafter are referred to as the Green Isolate and the White Isolate.

On April 24, 1976, both experimental birds were taken from the "white-noise room" and placed in an outdoor aviary at the Kalbfleisch Station. The aviary was within the territory of a wild Wood Thrush that arrived during the first week of May and could be heard regularly thereafter. Green was found dead in the aviary on June 6, 1976; an autopsy revealed a broken neck, possibly sustained as the result of a disturbance the previous night. He proved to be a male, with testes fully enlarged and measuring 11 mm. x 7 mm. at time of death. White remained in the aviary until early July, and then was donated to the New York Zoological Society for display at the Bronx Zoo. Its sex was not determined.

Hand-Rearing Equipment and Procedure

Eggs and young, up to the time that the birds were feeding for themselves, were kept in an isolation chamber designed by William Fish of Carmichael, California. This chamber consists of three plywood units that nest within one another, with an air space separating each of the units (fig. 1). The internal dimensions of the inner unit, which served as the actual cage, are 50 cm. by 47 cm. by 30 cm. Fish maintains that the net attenuation of sound in this chamber is on the order of 60 decibels. My own tests involving the monitoring of playback of avian vocalizations from within and without the chamber convinced me that the isolation of birds held under these conditions was more than adequate for the purposes of this study.

During the period that the eggs were incubated artificially, the Fish chamber was adapted to serve as a still-air incubator by suspending a thermostatically controlled electric heating element (no. 4 heater assembly, manufactured by the Lyon Rural Electric Co. of San Diego) from the ceiling of the inner unit, and by disconnecting the chamber's ventilation system temporarily. Air temperature was registered by a sensor positioned at the upper level of the

FIG. 1. Vernia Lanyon maintains a detailed log of the feeding schedule and the development of the experimental Wood Thrushes. An isolation chamber, upper left, was used as a still-air incubator and brooder. Honey bee pupae removed from the brood frame, rear center, were used to supplement the artificial diet of the isolates during their first week.

eggs (fig. 2) and monitored outside the chamber on a remote reading telethermometer. The thermostat, located as close to the eggs as possible, was adjusted to provide for a range in air temperature of from 37° C. to 39° C. (*ca.* 98° F. to 102° F.) at the level of the eggs and in a closed chamber. Following hatching, the thermostat was readjusted daily to provide for progressively lower ranges in air temperature at the level of the nestlings in a closed chamber:

First day and night, 34° C. to 37° C. (*ca.* 93° F. to 98° F.)

Second day and night, 32° C. to 35° C. (*ca.* 90° F. to 95° F.)

Third day and night, 29° C. to 32° C. (*ca.* 84° F. to 90° F.)

Fourth to eighth day, 26° C. to 29° C. (*ca.* 79° F. to 84° F.)

The heating element was removed on the eighth day, for nestlings are capable of thermoregulating at this age, providing they are not exposed to drafts or chilling below normal room temperature.

Containers of water placed within the inner unit provided moisture through evaporation (fig. 2). A small crystal of copper sulphate in each water container prevents growth of molds. I used a dial hygrometer (Abbeon Supply Co., Jamaica, N.Y.) to monitor relative humidity within the inner unit. The number of containers of water was adjusted to maintain a relative humidity of approximately 70 percent. The eggs were turned several times daily to prevent adhesion of membranes and provide exercise for the developing embryos. The relative humidity within the inner unit during the nestling

period was considerably lower because the ventilation system was activated after hatching, thus insuring a constant circulation of fresh air from the air-conditioned laboratory. The containers of water were removed several days prior to fledging. Formerly, I advocated (Lanyon and Lanyon, 1969, 1971) the use of round-bottomed heating mantles, as used in the chemistry laboratory for heating flasks of inflammable fluids, to "brood" the nestlings. Subsequently, I found that this was not only unnecessary but actually undesirable because of various risks inherent in the use of such mantles and the difficulties in maintaining a constant power supply and a safe brooding temperature. In the case of the Wood Thrushes (and six other species of songbirds that have subsequently been raised successfully from the egg stage in my laboratory) the electric element that provided the heat for artificial incubation was retained during the first few days following hatching as the source of heat for keeping the nestlings warm. It was removed from the chamber when the nestlings were capable of thermoregulation (on the eighth day in the case of the Wood Thrushes). The round-bottomed heating mantles, no longer used as a source of heat, do make excellent artificial nests, however, and I have continued to use them for the support of both eggs and nestlings. The removable tray that serves as the floor of the inner unit of the chamber is lined with a piece of Astro Turf, landscape surface (a molded polyethylene pile manufactured by Monsanto). This makes a superior cage bottom for it is nontoxic, resistant to fungal growth, permits fecal material to settle within the pile, provides for a gentle scouring and cleaning action on the birds' feet, and can be cleaned readily in an ordinary household washing machine.

FIG. 2. The two experimental Wood Thrushes are fed on the second day following hatching in the isolation chamber. Containers of water at the left provide moisture through evaporation. Air temperature is registered by the sensor at the rear of the "nest."

When the young Wood Thrushes were able to feed for themselves, at three weeks of age, they were transferred from the isolation chamber to a "white-noise room" where the motor noise from a powerful air-conditioning unit and a constant tone (at about 500 Hz.) from a signal generator effectively masked all sounds from outside the room, thereby maintaining the integrity of isolation from other birds. Within this room the birds were housed in two connecting plywood and wire-fronted cages, built at the Kalbfleisch Station, and each measuring 65 cm. by 35 cm. by 30 cm. The cage bottoms were lined with Astro Turf. Room temperature varied from 16° C. to 27° C. (*ca.* 60° F. to 80° F.). Though no attempt was made to reproduce the photoperiodic conditions that would be experienced by Wood Thrushes on migration or on the wintering ground, care was taken to insure a progressively increasing daylength in spring, thus approximating the conditions normal for temperate latitudes at that season.

During April and May 1975, when the isolates were nearly one year old, they were returned to a Fish isolation chamber where they could be tape recorded by means of a low impedance dynamic microphone installed at the rear of the chamber's inner unit. Recordings were made monaurally on a Uher 4400 Report Stereo, operating at 19 cm. per second, and later analyzed with a Kay Elemetrics' audio spectrum analyzer, Sona-Graph Model 6061B. Similarly, recordings were made a year later, in April 1976, when the birds were nearly two years old but still without exposure to other birds.

The dimensions of the outdoor aviary into which the Wood Thrushes were placed on April 24, 1976, were 5.0 m. by 2.5 m. by 2.0 m. The aviary was situated within the territory of a wild Wood Thrush, KFRS 2, whose songs were included in my analysis of wild bird songs. Additional tape recordings were made of the experimental birds in the outdoor aviary, with an Altec 660B microphone (low impedance setting and a long microphone cable).

Diet and Feeding Technique

I have experimented extensively with nestling diet and have greatly improved the technique from that reported in Lanyon and Lanyon (1969). The first innovation was the development of a more simplified recipe for a nestling soft bill mix (NSBM) used daily throughout the nestling and fledgling period, and this was reported in Lanyon and Lanyon (1971). The NSBM used for the Wood Thrushes and all species raised subsequently in my laboratory is the following recipe, which makes approximately six cups of food:

325 gm. (11.5 oz.) round steak (uncooked; all fat removed)

5 hardboiled eggs, without shells

2 cups turkey starter mash (a medicated poultry feed consisting of 28 percent crude protein available at most animal feed stores; sifted to eliminate coarser particles)

1 7.5 oz. jar of "Junior" grade carrots (prepared by Gerber)

3 tablespoon wheat germ

No water is required other than that contained in the above ingredients. These ingredients are forced through a food grinder and homogenized as thoroughly as possible. The recipe is made in bulk, frozen in small plastic containers, and then thawed as needed.

The following supplements to the NSBM were given to the nestlings and fledglings:

Multi-vitamin preparation (I use Hudson's Vi-Tot Drops; each bird receives one drop, with the NSBM, twice daily)

Calcium phosphate powder (packed by Richard Rover Co., East Rutherford, New Jersey; each bird receives a feeding of NSBM "dusted" lightly with this powder, twice daily)

Grit (I use Hartz Mountain; sifted to eliminate coarser particles; each bird receives a few grains with the NSBM, twice daily)

The second development in the simplification of the nestling diet was the elimination of all living food. In Lanyon and Lanyon (1969, 1971), I advocated daily supplements of pupae of the honey bee (*Apis mellifera*), but had recommended a gradual reduction so that by the time the young birds are feeding for themselves (about three weeks of age for many passerines) the living food has been phased out. In subsequent years I have placed less and less emphasis on the importance of honey bee brood. The young Wood Thrushes in this study were given

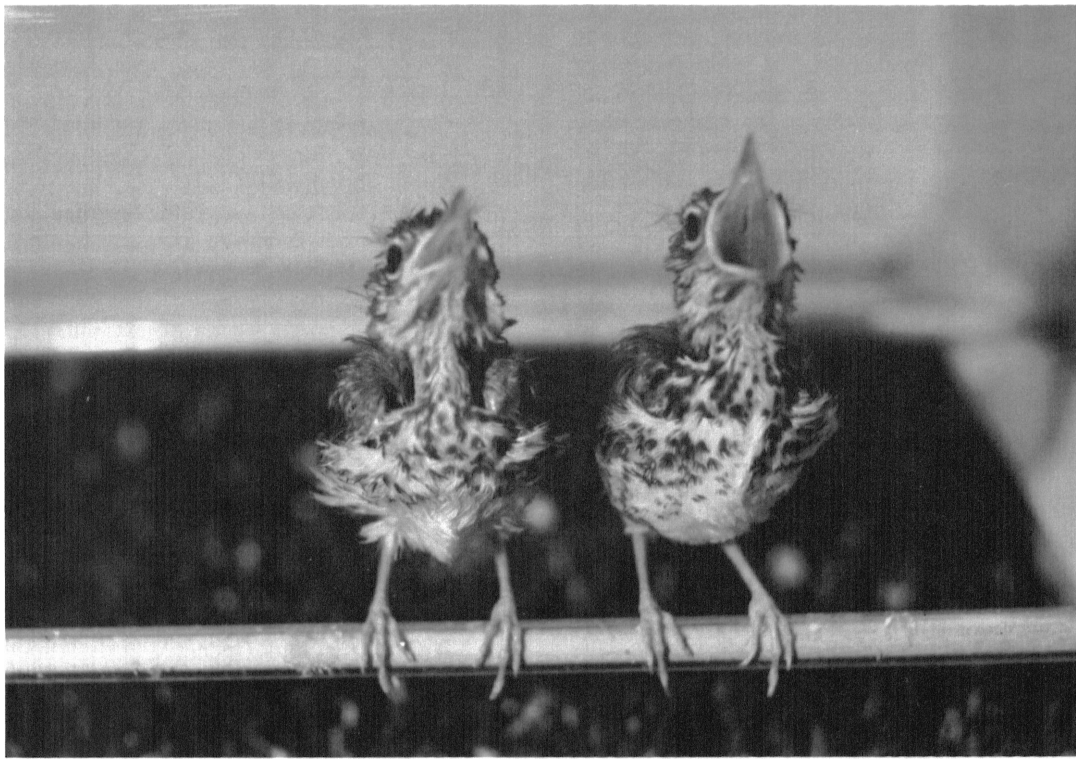

FIG. 3. The isolates at 18 days are not yet feeding for themselves and are still housed in the isolation chamber.

bee pupae only on the first seven days. More recently, I have successfully hand-reared Red-winged Blackbirds (*Agelaius phoeniceus*) and hybrid Eastern and Western Meadowlarks (*Sturnella magna* x *S. neglecta*) from the egg stage without any supplement of living food. From the time of hatching through to independence, these birds received nothing but NSBM plus the three supplements as prescribed above.

The simplification in the recipe for NSBM and the elimination of living food made it feasible to experiment with techniques and feeding schedules for administering food to nestlings. Small forceps were used to offer food to the Wood Thrushes (fig. 2), and the feeding schedule was that recommended in Lanyon and Lanyon (1971). But a major concern, particularly during the first few days following hatching, is that the nestlings receive a sufficient quantity of food to sustain their rapid growth, and this is especially difficult to achieve with small forceps. In recent years I have been using a plastic syringe that has had the opening somewhat enlarged with a small jeweler's drill. A syringe with a capacity of 1 cc. is appropriate for recent hatchlings of warbler-sized passerines; 3 cc. or 5 cc. syringes can be used for larger nestlings. Caution should be exercised to have the rubber plunger lubricated adequately to insure a smooth, controlled operation. The NSBM, including supplements as needed, is moistened with water and worked into a consistency that can be administered with the syringe without clogging on the one hand, or flowing uncontrollably on the other. Forceps can be used for feeding older and larger nestlings.

The frequency of feeding is best determined by the nestlings themselves and should be adjusted so that each nestling voids a fecal sac in response to each feeding. The actual timing

will vary with the age of the nestling and with the quantity of food administered through the syringe. The Wood Thrushes were fed every hour at first but this rate was gradually decreased to every two hours by the time they fledged. The birds were fed from 6:00 A.M. until 9:00 P.M.; all-night feeding is not necessary providing the birds are healthy.

When the Wood Thrushes were feeding for themselves, at three weeks of age, a standard soft bill mix (SBM) was substituted for the NSBM. This SBM is a modification of that fed to insectivorous birds at zoological parks and by aviculturists around the world, and has been modified slightly since my earlier papers. It too is made up in bulk, frozen, then thawed as needed. The following recipe makes approximately six quarts of SBM:

8.5 cups turkey starter mash
6 hardboiled eggs, with shells
3 14 oz. cans cooked horsemeat (minimum of 12% crude protein)
1 7.5 oz. jar of "Junior" grade carrots
0.5 cup wheat germ
0.5 of a 15 oz. box of seedless raisins

These ingredients are forced through a food grinder and mixed thoroughly. No water is required other than that contained in the ingredients. A dish of fresh SBM, with a very light "dusting" of a vitamin/mineral powder supplement (I use Theralin, manufactured by Lambert-Kay) was provided daily, along with a dish of drinking water containing several drops of the multi-vitamin preparation. The Wood Thrushes received no live food supplements to the SBM until they were nearly two years old and placed in an outdoor aviary. At that point they foraged in the ground litter, in addition to feeding on the SBM that continued to be provided daily.

Playback Experiments with Wild Birds

I conducted experiments at the Connetquot River State Park in early summer of 1976 to determine whether wild Wood Thrushes would respond to playback of the songs of the isolates. Five standardized playback tapes, each five minutes in length, were prepared from the following recordings:

1. Wild Wood Thrush (KFRS 1) on territory at the Kalbfleisch Field Research Station, recorded June 17, 1976.
2. Green Isolate at one year, recorded within the isolation chamber May 18, 1975.
3. Green Isolate at two years, recorded May 28, 1976, after three weeks of exposure to a wild Wood Thrush (KFRS 2).
4. White Isolate at two years, recorded June 10, 1976, after one month of exposure to a wild Wood Thrush (KFRS 2).
5. White Isolate at two years, recorded June 28, 1976, after seven weeks of exposure to a wild Wood Thrush (KFRS 2).

Most experiments involved the simultaneous playback of two of these standardized tapes on two Uher tape recorders without additional amplification. Speaker cables permitted operation of the recorders at 50 foot distances from two Electrovoice speakers set on the ground approximately 100 feet apart. Thus the "experimental area" was roughly that area within a rectangle that measured about 200 feet long and 100 feet wide. No visual stimuli (mounted birds or models) were provided. After the first five minutes of playback, the cables of the two speakers were interchanged, so that during the remaining five minutes of the experiment the positional sources of the two sets of auditory stimuli were reversed from those of the first five minutes. Each experiment thus provided two opportunities to observe orientation by territorial birds to one or the other of the two playback tapes: an initial orientation at the commencement of playback, and a second or reorientation following the interchange of speaker cables. This is a modification of a technique that I developed and have used successfully in systematic studies (Lanyon, 1963, 1967, 1978).

Notes were taken of the responses of the territorial birds, particularly with respect to their singing and their orientation or changes in orientation to one or both speakers. A bird was considered to have responded to playback if it oriented to the speaker and remained within a 50 foot radius of that speaker for all or nearly all of the five-minute period during which the playback emanated from that location. There is confirmation of this response and of the ability to discriminate between the two tapes when the bird reorients to the other speaker following the

interchange of the speaker cables. Each response could be further characterized according to intensity of song and to whether the bird actively engaged in short flights ("criss-cross") in the vicinity of the speaker or flew directly at and over the speaker ("pass"). A position at "midpoint" was one approximately equidistant from the two speakers.

In some of the experiments I varied the technique and used only a single playback tape, to establish the response to a particular tape without competition from the simultaneous playback of a second tape. If the single tape was played for five minutes, only a single speaker was used; but in those instances when it was desirable to establish reorientation to a new location, a second speaker was used for the second half of the 10 minutes of playback. On occasion, when only a single playback tape was used, I would simply use the Uher's speaker and walk through the territory of the wild bird. Thirty-seven playback experiments were conducted with five different Wood Thrushes during the period from June 25 to July 2, 1976. None of these wild birds was color-banded, but each could be identified individually by its distinctive and unique repertoire of song patterns. Excerpts from my field notes are included to illustrate the responses of these wild birds.

RESULTS

Song of the Wood Thrush

No one has improved on the description of the song of the Wood Thrush as given by Saunders (1924):

> Each [song] may have three parts, an introduction of two or three short notes, usually low in pitch and not especially musical; a central phrase of two to five notes, most commonly three, loud, clear, flute-like and extremely musical; and a termination of three or four notes, usually high-pitched, not so loud, and generally the least musical part of the song. [Songs] may be sung either with or without either introduction, termination, or both . . . The central phrases . . . are the most noticeable part, and since they are louder and carry farther, are sometimes the only part heard. Each bird has from two to nine different [central phrases]. They are sung in no definite order, but it is not common for one phrase to be repeated immediately without some other intervening. The bird usually shows preference for one or two of its phrases and sings them more frequently than others. There are, in normal birds, two or three introductions and four or five terminations, and these are sung with first one [central] phrase and another, then omitted entirely. The individual may be identified by central phrases alone, but the addition of introductions and terminations to the record will make one double certain of the identification [to individual].

Saunders also suggested that individual Wood Thrushes could best be identified not by the exact pitches of the phrases but rather the forms of the phrases and their relation to each other, and also by the number of phrases (repertoire size) sung.

Borror and Reese (1956) confirmed Saunders' findings with a sound spectrographic analysis of tape recordings of Wood Thrushes in Ohio. These authors were the first to demonstrate that the Wood Thrush is capable of producing two series of notes simultaneously. Greenewalt (1968) argued convincingly that these signals, overlapping in time, arise separately from the two bronchial sections of the syrinx. Though he found this phenomenon more common among birds than had been previously appreciated, Greenewalt considered the Wood Thrush to be "without doubt the most versatile and accomplished 'internal duettist.' Almost without exception the final phrase of its song involves both sources, each producing harmonically unrelated phrases with complex modulations. . . . Even in the 'central' or musical portion of the Wood Thrush song, both voices are frequently employed."

In this study I was able to record and graph the songs of seven wild Wood Thrushes, as a basis for an analysis of the performance of the isolates. The songs in my samples typically consist of three phrases (identified in fig. 4:1). Each of these phrases is characterized by notes that are unique, i.e., do not contribute to the other two phrases.

(1) An *introductory phrase*. Each song normally begins with from one to four notes characterized by their low frequency, low intensity, and brief duration, relative to the notes in the remainder of the song. A male typically has

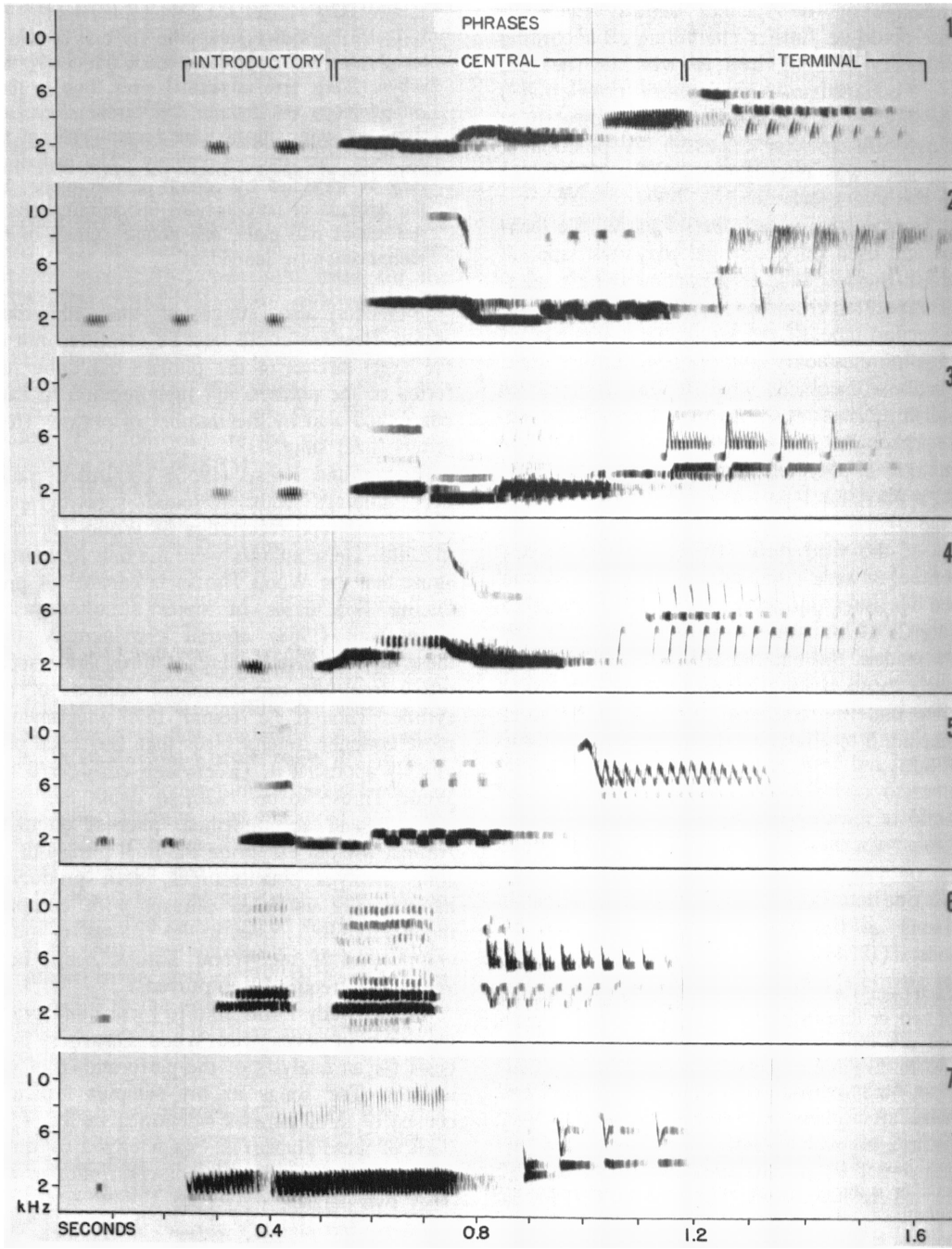

FIG. 4. Examples of songs of five wild Wood Thrushes (1-5) and of the experimental isolates (6-7). Introductory, central, and terminal phrases are identified in 1.

one or two types of notes that it uses in the introductory phrase (one male in my sample had three), but only one of these basic types is used, and sometimes repeated, in any given rendition of a song pattern. An introductory phrase may be lacking in some songs and be present in the same basic song patterns rendered at other times. As Saunders has noted, the introductory phrase is that part of the Wood Thrush song that is most likely to be missed by the human ear due to the low intensity with which it is rendered. It is of no aid in the identification of individual males for there is no significant difference between the notes of individuals. Examples of introductory phrases are given in figure 4. Introductory phrases have been purposely omitted from many of the song patterns illustrated here, in the interests of simplifying the displays and maximizing the scale of reproduction.

(2) A *central phrase*. The great intensity and clarity of the flutelike notes of the central phrase are apparent in the songs of five different wild birds in figure 4:1-5. Due to this intensity and musical quality, and the fact that it may be rendered alone, without an accompanying introductory or terminal phrase, the central phrase can be used as a convenient basis for classifying the songs in the repertoire of any given male. The seven males in my study had from three to five basic types of central phrases, with an average of 3.9. These phrases averaged from 0.57 to 0.79 second in duration among the seven males (table 5). No song contained more than one type of central phrase, nor was there any instance of the repetition of one of these basic types within a given song. My samples confirm Saunders' (1924) and Borror and Reese's (1956) conclusion that individuals may be identified by central phrases alone, for no two males had identical central phrases, and only two males had more than two central phrases (within their repertoires of from three to five phrases) that were at all similar in their spectrographic configuration. Nearly all the central phrases in my sample from seven wild birds contain overlapping, harmonically unrelated notes; this phenomenon is particularly noticeable in the central phrases in figure 4:4 and in figure 9:1.

(3) A *terminal phrase*. The seven males in this study had from six to nine distinct types of phrases that they used for the terminal portions of their songs, with an average of 7.9 terminal phrases. These terminal phrases usually involve higher frequencies and are not so loud nor as musical as the central phrases. They generally sound noisy to the human ear, due to their broad frequency spectrum, and they often have a rasping quality due to rapid modulation of the component notes. It is here that the remarkable property of an independently and simultaneously produced series of sound signals is carried to the extreme, for it appears that each of the two signal generators in the syrinx is capable of contributing a highly complex, continuous or pulsed signal to this terminal phrase. Examples of terminal phrases, all with dual signals, are illustrated in the song patterns of wild Wood Thrushes in figure 4:1-5. Terminal phrases among the seven wild males averaged from 0.37 to 0.59 second in duration (table 5).

In concern for the adequacy of my samples to demonstrate the complete repertoire of phrases for each of these seven wild Wood Thrushes, I plotted the number of renditions of song recorded in each sample before all of the known phrases for each male had been expressed (fig. 5). No bird took longer than 34 renditions of song to give his complete repertoire of all phrases (introductory, central, and terminal). Since the shortest of the sample bouts recorded from these seven birds was one of 56 renditions, the samples appear to have been adequate to demonstrate individual variability. Table 1 shows the extent of this variability within the repertoires of these birds. Each wild bird had, on average, 13.7 different types of phrases that were sung in various combinations to form an average of 14.4 different patterns of song. The frequency with which each phrase type was used by these wild birds is revealed in table 2. Whereas each bird favored the use of one of its introductory phrases, there was no comparable disparity in the frequency with which the various types of central and terminal phrases were used, for there is only a gradual decrease in frequency when these phrase types are ranked according to frequency of use. Likewise there is only a

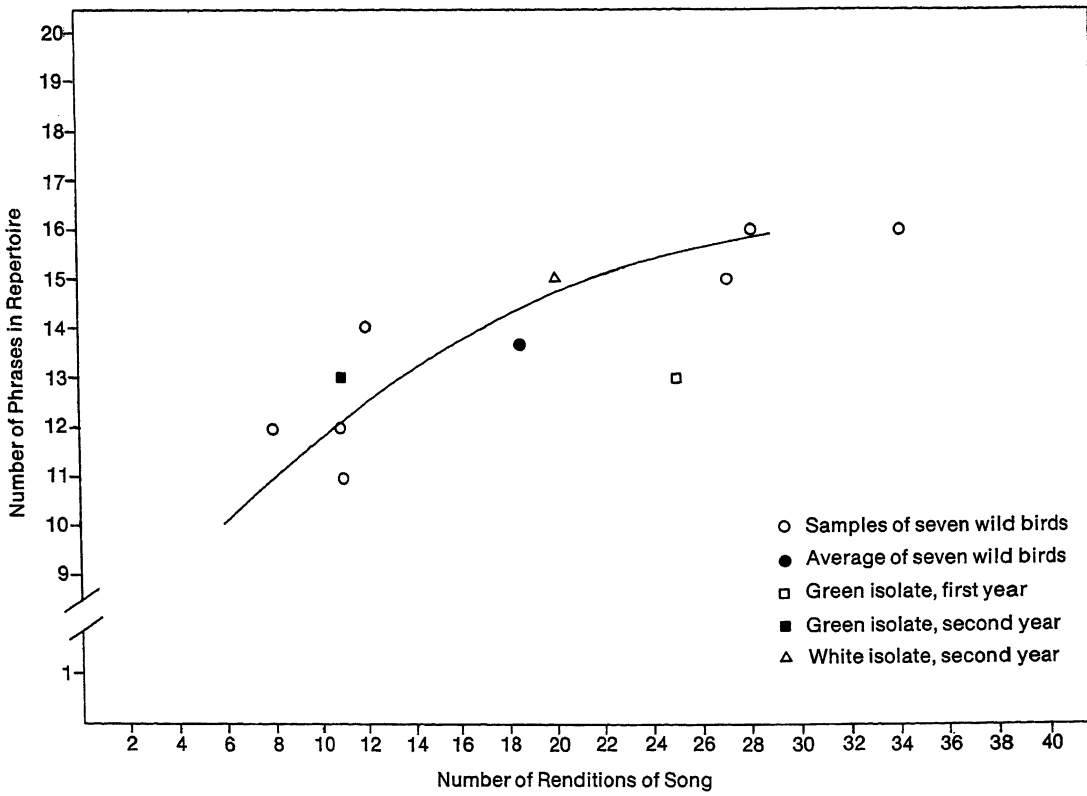

FIG. 5. The number of renditions of song required for the expression of the complete repertoires of phrases recorded from each of the seven wild birds and from the two isolates.

TABLE 1

Variability in the Repertoires of Seven Wild Birds and Two Isolates

Sample	Number of Renditions of Song Recorded	Number of Song Patterns	Number of Phrases	Number of Introductory Phrases	Number of Central Phrases	Number of Terminal Phrases
CRSP 1	137	19	16	3	4	9
CRSP 2	56	17	14	2	3	9
CRSP 3	63	9	12	2	3	7
CRSP 4	90	16	16	2	5	9
CRSP 5	80	16	15	2	5	8
KFRS 1	132	14	11	2	3	6
KFRS 2	99	10	12	1	4	7
Average for Seven Wild Birds	93.9	14.4	13.7	2.0	3.9	7.9
Green Isolate, first year	72[a]	28[a]	13	1	4	8
Green Isolate, second year	61	15	13	1	4	8
White Isolate, June 10, 1976	141[a]	24[a]	15	2	5	8
White Isolate, June 28, 1976	97[a]	22[a]	15	2	5	8

[a]Does not include renditions of isolated phrases and patterns lacking central phrases.

TABLE 2
Frequency (in Percentage of Song Renditions) of Use of Phrase Types in Samples of Seven Wild Birds

Sample	Introductory Phrases	Central Phrases	Terminal Phrases
CRSP 1	(none, 70.1)[a]		(none, 41.7)
	1.[b] 63.4	1. 28.4	1. 18.7
	2. 19.5	2. 27.0	2. 15.0
	3. 17.1	3. 23.4	3. 11.3
		4. 21.2	4. 10.0
			5. 10.0
			6. 10.0
			7. 8.8
			8. 8.8
			9. 7.4
CRSP 2	1. 73.2	1. 35.7	1. 19.6
	2. 26.8	2. 33.9	2. 17.9
		3. 30.4	3. 10.7
			4. 10.7
			5. 10.7
			6. 8.9
			7. 8.9
			8. 8.9
			9. 3.7
CRSP 3	1. 98.4	1. 38.1	1. 17.4
	2. 1.6	2. 34.9	2. 15.9
		3. 27.0	3. 14.3
			4. 14.3
			5. 12.7
			6. 12.7
			7. 12.7
CRSP 4	(none, 27.8)		
	1. 93.8	1. 37.8	1. 27.8[c]
	2. 6.2	2. 30.0	2. 14.4
		3. 14.4	3. 12.2
		4. 11.1	4. 12.2
		5. 6.7	5. 11.1
			6. 11.1
			7. 11.1
			8. 10.0
			9. 8.9
CRSP 5	(none, 1.3)		(none, 1.3)
	1. 82.3	1. 25.0	1. 26.6
	2. 17.7	2. 23.8	2. 21.5
		3. 20.0	3. 12.7
		4. 16.2	4. 11.4
		5. 15.0	5. 10.1
			6. 10.1
			7. 5.1
			8. 2.5
KFRS 1			(none, 10.6)
	1. 95.5	1. 38.6	1. 22.9[c]
	2. 4.5	2. 32.6	2. 17.8
		3. 28.8	3. 16.9
			4. 16.9
			5. 15.3
			6. 11.0
KFRS 2	(none, 87.9)		
	1. 100.0	1. 31.3	1. 22.2
		2. 28.3	2. 18.2
		3. 25.2	3. 14.2
		4. 15.2	4. 13.1
			5. 13.1
			6. 10.1
			7. 9.1

[a]Songs lacking a phrase were excluded from the analysis of frequency of use; thus, 70 percent of the songs of CRSP 1 lacked introductory phrases, and phrase type 1 was used in 63 percent of the remaining songs in the sample, i.e., those songs having an introductory phrase.

[b]Phrases have been assigned numbers that correspond to their rank in terms of frequency of use.

[c]Some songs contained two terminal phrases, thus frequency of use of this set of phrases exceeds 100 percent.

gradual decrease in frequency when the different patterns of song are ranked according to frequency of use, i.e., no one pattern of song is heavily favored to the exclusion of others in my samples of wild birds (table 3). As Saunders (1924) and Borror and Reese (1956) observed, there is no predictable order or sequence in which the song patterns are sung, and rarely is a given pattern repeated before the rendition of another pattern.

Songs of the Green Isolate at One Year of Age

Of the two isolates, only Green sang at one year of age. So consistent were my observations of singing behavior from Green and the complete lack of song from White in 1975 that I concluded I had reared a male and a female. I interpreted the obvious dominance of Green over White as additional support for the conclusion that White was a female, but the birds were too valuable to risk surgery for a positive determination of sex. The fact that only one of the isolates was singing during their first spring, for whatever reason, was gratifying from an experimental standpoint for it eliminated the possibility that auditory feedback or

TABLE 3

Frequency (in Percentage of Song Renditions) of Use of Song Patterns in Samples of Seven Wild Birds and Two Isolates

Song Patterns, Identified by Rank According to Frequency of Use

Sample	1	2	3	4	5	6	7	8	9	10	11	12
CRSP 1	22.6	11.0	8.0	6.6	6.6	5.8	5.1	5.1	5.1	5.1	4.4	4.4
CRSP 2	16.1	8.9	8.9	8.9	8.9	7.1	7.1	5.4	5.4	5.4	3.6	3.6
CRSP 3	15.9	14.3	12.7	12.7	12.7	12.7	12.7	4.8	1.6	—	—	—
CRSP 4	10.0	10.0	10.0	10.0	10.0	8.9	8.9	8.9	4.4	4.4	4.4	3.3
CRSP 5	12.5	12.5	10.0	10.0	10.0	8.8	8.8	7.5	3.7	3.7	3.7	2.5
KFRS 1	17.4	15.2	12.9	12.9	10.6	9.1	9.1	5.3	2.3	2.3	0.7	0.7
KFRS 2	22.2	18.2	10.1	10.1	10.1	9.1	8.1	5.1	4.0	3.0	—	—
Average for 7 wild birds	16.7	12.9	10.4	10.2	9.8	8.8	8.5	6.0	3.8	3.4	2.4	2.1
Green Isolate, first year	22.2	9.7	8.3	6.9	5.6	4.2	4.2	2.8	2.8	2.8	2.8	2.8
Green Isolate, second year	19.7	13.1	13.1	11.5	6.6	6.6	4.9	4.9	4.9	3.3	3.3	3.3
White Isolate, June 10	10.6	10.6	9.2	8.5	7.8	7.1	7.1	6.4	5.7	5.0	3.5	2.8
White Isolate, June 28	13.4	10.3	9.3	7.2	7.2	6.2	6.2	5.2	5.2	5.2	5.2	3.1

stimulation from a sibling would be a factor in the development of song.

Green's singing during his first spring was characterized by "experimentation." This involved the frequent rendition of isolated phrases, i.e., not in normal combination with other phrases to form complete song patterns, and the delivery of many variations of the same basic phrase type. Song patterns sometimes lacked central phrases, contained repetitions of the same central phrase, or included combinations of two central phrases. I recorded a sample of songs in May (1975) when it became apparent that the transition from subsong to definitive song had progressed as far as it was going to that season. Isolated phrases and song patterns lacking central phrases were still being delivered on occasion, but these were not included in my analysis of definitive song.

Most of the songs of Green at one year of age are recognizable (to the human ear) as Wood Thrush; they have a basic structure, syntax, and rhythm similar to that of wild birds, i.e., they are normally composed of introductory, central, and terminal phrases with characteristics similar to those that I have identified for the species. Both the central and terminal phrases contain two simultaneous signals with unrelated frequencies, a characteristic of the species. But there is a greater than normal variability in the spectrographic configuration of all phrase types, among the various songs in which they appear, and my sample recording contains 28 different song patterns (i.e., different combinations of these phrase types), nearly twice as many as the average to be expected from a wild Wood Thrush (table 1). The total repertoire of 13 phrase types is average for the species, however, and these are distributed in a normal manner among introductory, central, and terminal phrases (table 1).

The frequency of use of the various phrase types and song patterns at one year of age does not differ significantly from that exhibited by wild birds (tables 3 and 4), though the frequency with which many of the isolate's songs are sung is diluted due to the greater number of different patterns in the isolate's sample. Figures 6 (1, 3, 5, 7) and 7 (1, 3, 5, 7) illustrate the complete repertoire of four central and eight terminal phrases in the songs of the Green Isolate at one year of age.

TABLE 3 — *(Continued)*

13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
3.7	2.9	0.7	0.7	0.7	0.7	0.7	—	—	—	—	—	—	—	—	—
3.6	1.8	1.8	1.8	1.8	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.2	2.2	1.1	1.1	—	—	—	—	—	—	—	—	—	—	—	—
2.5	1.3	1.3	1.3	—	—	—	—	—	—	—	—	—	—	—	—
0.7	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.8	1.3	0.7	0.7	0.4	0.1	0.1	—	—	—	—	—	—	—	—	—
2.8	2.8	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4
1.6	1.6	1.6	—	—	—	—	—	—	—	—	—	—	—	—	—
2.8	2.1	2.1	2.1	1.4	0.7	0.7	0.7	0.7	0.7	0.7	0.7	—	—	—	—
3.1	2.1	2.1	2.1	2.1	1.0	1.0	1.0	1.0	1.0	—	—	—	—	—	—

The central phrases of the Green Isolate are less musical, more discordant, and simpler in pattern (i.e., exhibit less heterogeneity within each phrase) than the central phrases of wild Wood Thrushes. This can be appreciated by comparing the simple but discordant central phrase in figure 4:6 with the central phrases in figure 4:1-5. The central phrases differ further from those of wild birds by being significantly shorter in duration (table 5). Often one type of central phrase would be repeated within a single song pattern, as in figure 4:6, figure 6:5, 7, and figure 7:3, 5, 7. Different types of central phrases were sometimes rendered in a single song pattern, as in figure 8:1. Some of the song patterns lacked a central phrase, as in figure 8:2, and this reduction in the role of the central phrase is further demonstrated by the lack of isolated central phrases sung as complete songs, as is sometimes the case with wild Wood Thrushes. In some instances a central phrase and a terminal phrase were sung as a continuous unit, as in figure 8:5.

I am unable to detect any consistent differences between the terminal phrases of this isolate and those of wild Wood Thrushes with regard to characteristics of pattern configuration, general quality, or duration (table 5). The manner of delivery of these terminal phrases often differed from that of wild birds, however. Some song patterns consisted of isolated renditions of a terminal phrase, as in figure 8:3; others contained two terminal phrases, either rendered continuously (fig. 8:4) or independently (fig. 8:6). As noted above, a terminal phrase was sometimes given as a continuation of a central phrase, without interruption of the signal (fig. 8:5).

Songs of the Green Isolate at Two Years of Age

After exposure to wild birds at nearly two years of age, which included one month of exposure to a Wood Thrush (KFRS 2) on territory, the Green Isolate was recorded again. The usual spring transition from subsong to definitive song had been completed by this time, and there is little evidence in this sample of the "experimentation" that characterized the sample of song at one year of age. The number of basic song patterns is decreased from 28 to 15 (table 1), an average number for the species, by

a reduction in the number of combinations of terminal phrases and central phrases and a reduction in the use of more than one terminal phrase per song pattern. The song patterns retained in the second year are further simplified in many cases by a reduction in the repetitions of the central phrases. The frequency of use of these song patterns in this sample at two years of age is similar to the average for my samples of wild birds (table 3). The repertoire of phrases, of normal size during the first year, remained identical in the second year (table 1), and the frequency of use of these phrase types did not change significantly, with the same central and terminal phrases being dominant in both years (table 4).

The phrase types in this sample are the same as those used by the Green Isolate the year before, as illustrated in figures 6 and 7. No new phrases were added, even after exposure to the wild Wood Thrush (KFRS 2) in whose territory the aviary was located. Figure 9 illustrates the complete repertoire of four central and seven terminal phrases (introductory phrases have been omitted) of this wild Wood Thrush, as expressed in eight of its 10 different song patterns. The two missing song patterns of this wild bird combine (1) the central phrase of figure 9:5-7 with the terminal phrase of figure 9:4, and (2) the central phrase of figure 9:1 with the terminal phrase of figure 9:5. When one compares the central and terminal phrases of figure 9 with those in figures 6 and 7, there is no evidence that the Green Isolate was influenced by his exposure to the wild Wood Thrush.

Songs of the White Isolate at Two Years of Age

As noted above, the White Isolate was initially thought to be a female because of its complete lack of song at one year of age and its subordinate relationship with Green during the nearly two years that they were housed in

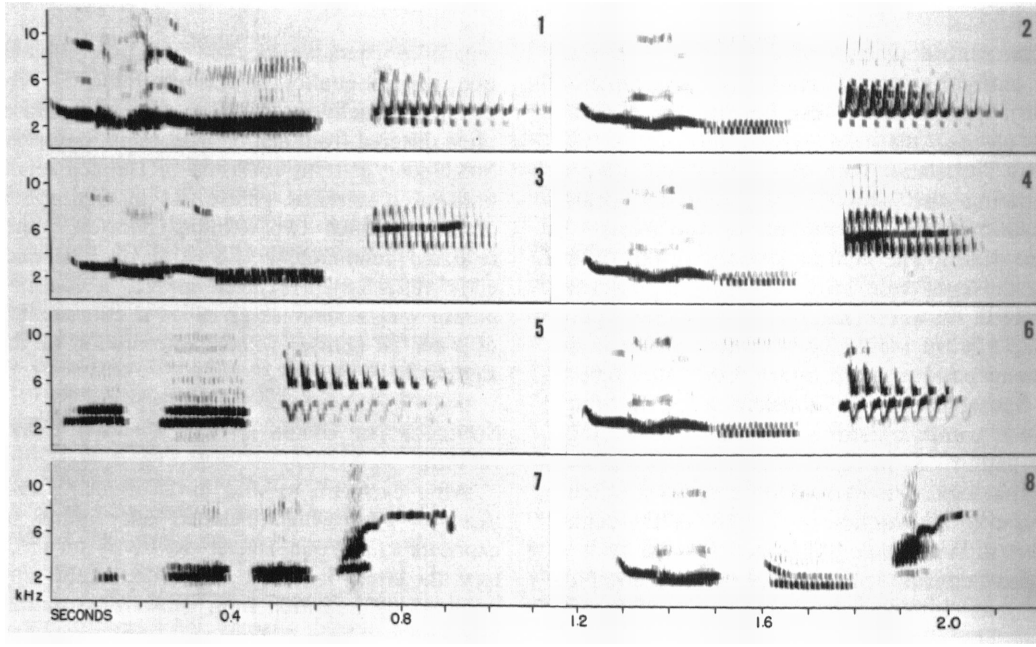

FIG. 6. Some songs of the Green Isolate at one year (1, 3, 5, 7) and at two years (2, 4, 6, 8) of age that illustrate, with those in figure 7, this isolate's complete repertoire of four central and eight terminal phrases. Introductory phrases have been omitted from these displays.

TABLE 4
Frequency (in Percentage of Song Renditions) of Use of Phrase Types in Samples of Two Isolates

Sample	Introductory Phrases	Central Phrases	Terminal Phrases
Green Isolate, first year			(none, 26.4)[a]
	1.[b] 100.0	1. (e)[c] 36.1	1. (l)[c] 18.9[d]
		2. (bc) 34.7	2. (m) 18.9
		3. (c) 19.4	3. (f) 17.0
		4. (b) 9.7	4. (o) 15.1
			5. (h) 15.1
			6. (g) 11.3
			7. (n) 7.5
			8. (i) 3.8
Green Isolate, second year	(none, 1.6)		(none, 4.9)
	1. 100.0	1. (bc)[c] 50.8	1. (l)[c] 21.5[d]
		2. (e) 29.5	2. (o) 17.5
		3. (c) 13.1	3. (h) 14.0
		4. (b) 6.6	4. (m) 12.3
			5. (g) 12.3
			6. (f) 8.8
			7. (n) 8.8
			8. (i) 8.8
White Isolate, June 10, 1976	(none, 11.3)		(none, 14.9)
	1. 91.5	1. (b)[c] 44.0	1. (g)[c] 18.3
	2. 8.5	2. (n) 21.3	2. (p) 15.8
		3. (c) 18.4	3. (o) 12.5
		4. (y) 8.5	4. (m) 12.5
		5. (v) 7.8	5. (t) 11.7
			6. (s) 10.8
			7. (f) 10.0
			8. (r) 8.3
White Isolate, June 28, 1976	(none, 38.1)		(none, 19.6)
	1. 81.7	1. (b)[c] 29.9	1. (g)[c] 16.7
	2. 18.3	2. (n) 28.9	2. (p) 16.7
		3. (c) 22.7	3. (o) 15.4
		4. (y) 10.3	4. (f) 12.8
		5. (v) 8.2	5. (r) 11.5
			6. (s) 10.3
			7. (t) 9.0
			8. (m) 7.7

[a]Songs lacking a phrase were excluded from the analysis of frequency of use; thus, 26 percent of the songs of Green isolate, first year sample, lacked terminal phrases, and phrase type 1 was used in 19 percent of the remaining songs in the sample, i.e., those songs having a terminal phrase.

[b]Phrases have been assigned numbers that correspond to their rank in terms of frequency of use.

[c]Central and terminal phrases have been assigned letters that identify them within the repertoires of phrases of each male, to permit comparison of frequency of use of phrase types in the two samples for each of the isolates.

[d]Some songs contained two terminal phrases, thus frequency of use of this set of phrases exceeds 100 percent.

TABLE 5
Duration of Central and Terminal Phrases (in Seconds)

	Central Phrases			Terminal Phrases		
Sample	Number	Mean	Range	Number	Mean	Range
CRSP 1	4	0.57	0.51-0.66	9	0.45	0.31-0.58
CRSP 2	3	0.69	0.66-0.74	9	0.51	0.35-0.54
CRSP 3	3	0.65	0.58-0.70	7	0.59	0.51-0.74
CRSP 4	5	0.62	0.58-0.66	9	0.53	0.35-0.74
CRSP 5	5	0.62	0.58-0.66	8	0.46	0.35-0.54
KFRS 1	3	0.79	0.66-0.97	6	0.52	0.47-0.66
KFRS 2	4	0.59	0.54-0.66	7	0.37	0.16-0.51
Green Isolate	4	0.42	0.30-0.48	8	0.37	0.19-0.51
White Isolate	5	0.48	0.33-0.58	8	0.47	0.39-0.56

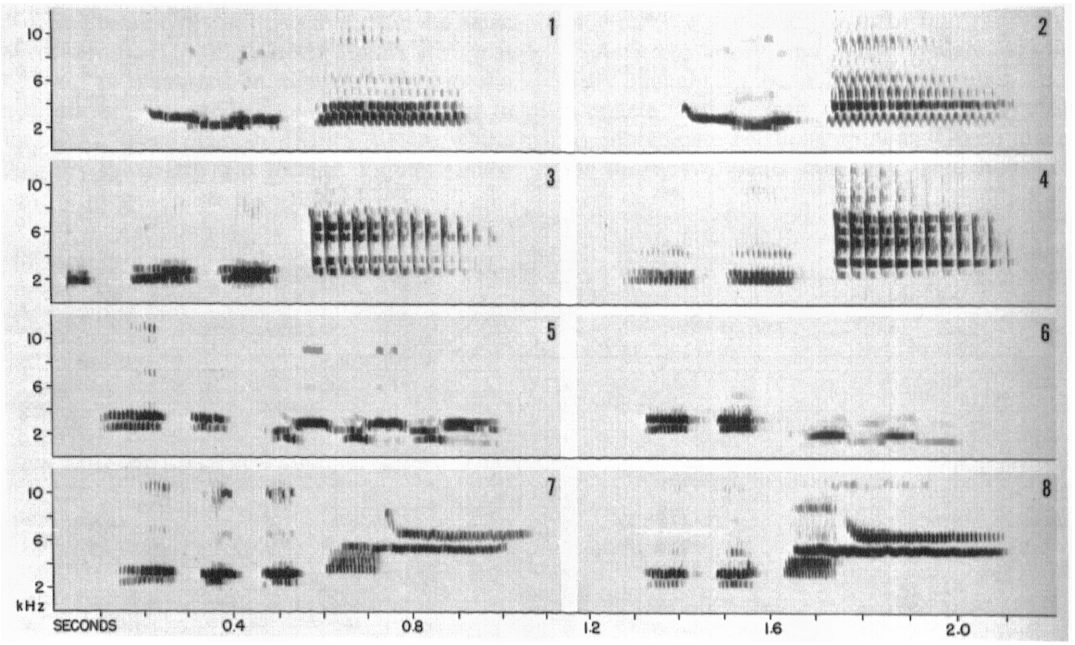

FIG. 7. Some songs of the Green Isolate at one year (1, 3, 5, 7) and at two years (2, 4, 6, 8) of age that illustrate, with those in figure 6, this isolate's complete repertoire of four central and eight terminal phrases. Introductory phrases have been omitted from these displays.

small but connecting cages. Shortly after both isolates were placed in a large outdoor aviary in April 1976, I observed that White as well as Green was giving subsong, and by late May some definitive song patterns could be heard from White, though much less frequently and for shorter periods of time than in the case of Green. It was not until Green died from an accident (?) in early June that White began to deliver extended bouts of definitive song,

which suggests that the behavioral dominance of Green may have been responsible for the suppression of song in White.

The delay in the full expression of song in White until that isolate was nearly two years old and had been exposed to wild birds thus provided the opportunity for comparing the performance of the two isolates under rather different experimental conditions. Two recordings of White were made in the outdoor aviary in June 1976. These samples of song, dated June 10 and June 28, were analyzed for evidence that White may have been influenced by (1) the songs of Green, the sibling isolate, and by (2) the songs of the wild Wood Thrush (KFRS 2) in whose territory the aviary was located.

Both samples of White's song bouts show evidence of "experimentation," including renditions of isolated phrases, patterns lacking central phrases, and a greater variety of song patterns than is characteristic of wild Wood Thrushes (table 1). This degree of variability is similar to that found in the recording of the Green Isolate at one year of age. White's song patterns have a basic structure, syntax, and rhythm similar to those of wild birds and of the Green Isolate, i.e., they are composed of introductory, central, and terminal phrases with characteristics similar to those that have been identified for the species, including dual, simultaneously produced signals. The total repertoire of phrase types is 15, about average for the species, and these are distributed in a normal manner among the three categories of phrases

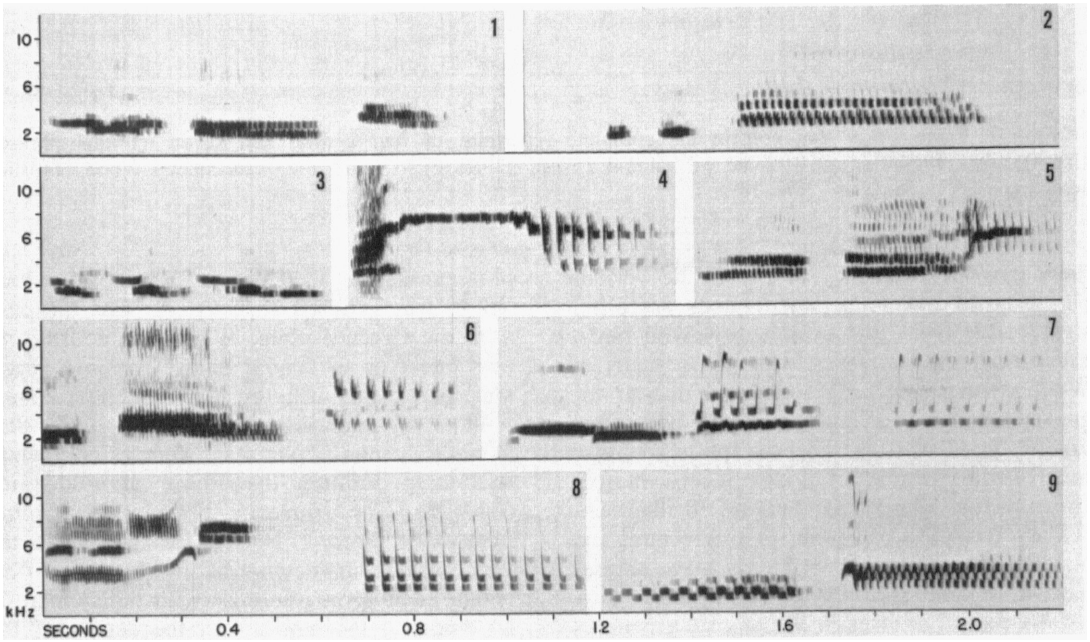

FIG. 8. Some abnormal characteristics of the phrases and song patterns of the two isolates, Green at one year of age (1-6), and White at two years of age (7-9): 1, use of three types of central phrases in one song; 2, song consists solely of the two notes of the introductory phrase and a terminal phrase, and lacks a central phrase; 3, song consists solely of an isolated terminal phrase; 4, combination of two terminal phrases, delivered without an interruption in the signal; 5, combination of a central and a terminal phrase, delivered without an interruption in the signal; 6, use of two independent terminal phrases; 7, repetition of a single terminal phrase within the same song; 8, two independent terminal phrases within the same song; 9, song consists of an abnormal introductory phrase and a terminal phrase, and lacks a central phrase.

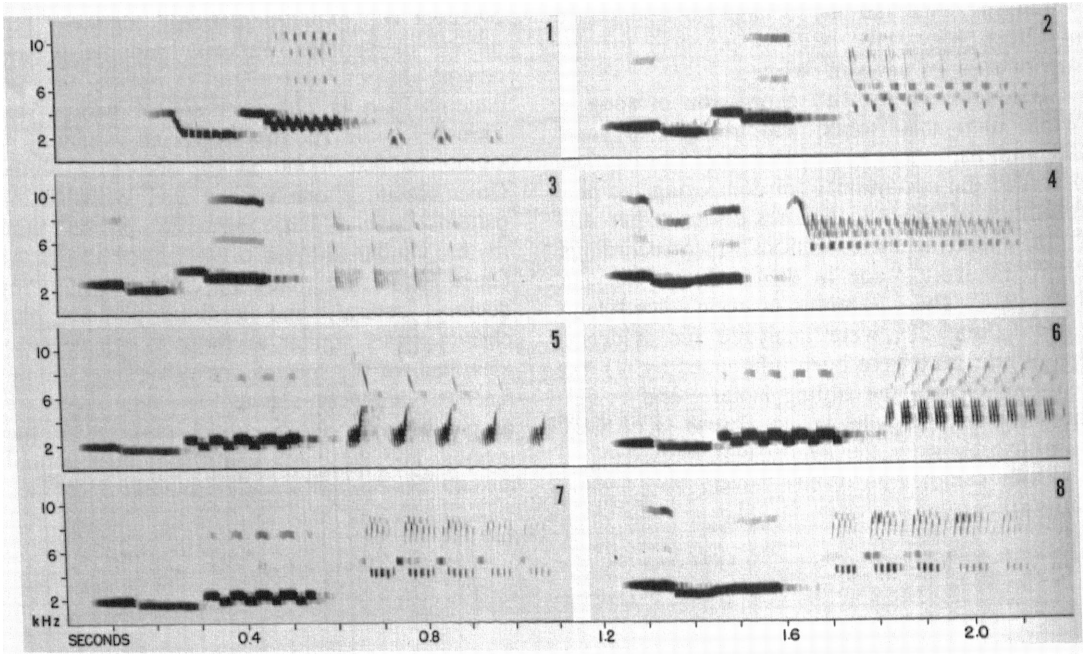

FIG. 9. Some songs that contain the complete repertoire of four central and seven terminal phrases (introductory phrases omitted) of the wild Wood Thrush (KFRS 2) to which the experimental Wood Thrushes were exposed in May and June 1976.

(table 1). The frequency of use of the various phrase types and song patterns does not differ significantly from that exhibited by wild birds, except that the frequency with which many of White's songs are sung is diluted due to the greater number of different patterns in its repertoire (tables 3 and 4). This exception was also true of the sample of songs recorded from Green at one year of age. Figure 10 illustrates White's complete repertoire of five central and eight terminal phrases (introductory phrases have been omitted).

The central phrases in White's song patterns have the same discordant, noisy quality, and lack of heterogeneity that characterized Green's central phrases—characteristics that distinguish both isolates from the wild birds that I recorded. Compare, for example, White's central phrase in figure 4:7 with the central phrases of wild birds in figures 4:1-5, or White's five central phrases in figure 10 with the four central phrases of the wild Wood Thrush to which White was exposed (fig. 9). As was the case with the Green Isolate, White would often repeat one type of central phrase within a single song pattern, as in figure 10:1, or deliver a song without a central phrase, as in figure 8:9. White's central phrases were significantly shorter in duration than those of wild birds (table 5). The similarity between the central phrases of the two isolates is confined to the very general characteristics that in turn differentiate them from those of wild birds; there is no evidence to suggest that the details of the patterns of White's central phrases were the result of imitation of Green. Nor is there any evidence that White imitated the wild Wood Thrush (fig. 9) in developing his central phrases.

I can detect no consistent differences between the quality and general characteristics of White's terminal phrases and those of wild

birds (or of the Green Isolate), but the two isolates and the wild Wood Thrush (KFRS 2) to which they were exposed appear not to share the detailed configuration of any particular terminal phrase.

Response of Wild Birds to Playback of Isolates' Songs

All five Wood Thrushes tested at the Connetquot River State Park responded to the control tape, i.e., to the songs recorded from one of the wild birds at the Kalbfleisch Field Research Station (KFRS 1). None of the five Connetquot birds responded to playback of the songs of the two isolates. This lack of response was demonstrated by all five birds to the tape of the Green Isolate at one year of age, by one bird to the tape of the Green Isolate at two years of age, by one bird to the tape of the White Isolate at two years of age (recording of June 10), and by three birds to the tape of the White Isolate at two years of age (recording of June 28). In those experiments in which there was simultaneous playback of the songs of the isolates and the songs of the wild Wood Thrush, all five of the Connetquot birds were able to discriminate between these tapes and responded only to the songs of the wild bird. In studies where there has been a bioassay of the performance of experimental isolates, the wild conspecifics generally do not respond in a normal manner to the playback of the isolate song (Thielcke, 1973; Shiovitz, 1975; Ewert, 1978).

The complete lack of response to the songs of the isolates in this study negated the need for a more quantitative approach to documenting the response of the wild conspecifics. The following series of four experiments, conducted with one of the Connetquot birds (CRSP 1) on June 25, 1976, illustrates the lack of response of these wild birds to the playback of the Green Isolate's songs at one year of age:

Experiment 1—Only one tape used: Green Isolate at one year. Only one speaker used. Start at

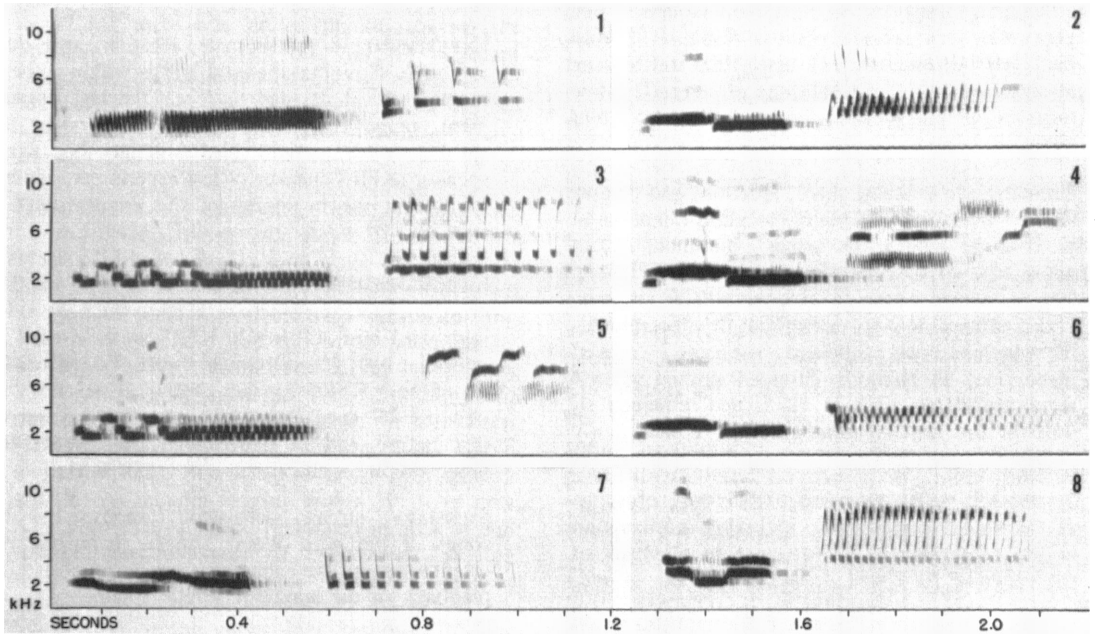

Fig. 10. Some songs of the White Isolate at two years of age that contain its complete repertoire of five central and eight terminal phrases (introductory phrases omitted).

10:40 A.M. Wild bird had been singing three minutes earlier, but location unknown at start. At 10:43, heard a bird singing outside experimental area; bird is within hearing distance of the playback, but showing no interest. No show by end of five minutes of playback.

EXPERIMENT 2—same male, location, and date as above. Tapes used: wild Wood Thrush (KFRS 1) vs. Green Isolate at one year. Wild bird silent, location unknown, at start at 10:47 A.M. Wild bird began to sing at once. It showed up at a perch 50 ft. from the KFRS speaker at 10:48. Pass over KFRS speaker at 10:50; still singing well. A crisscross at 10:50:30. Singing constantly. Out to 50 feet at 10:52, still singing, at cable switch. To midpoint by 10:53. In to 40 ft. of new KFRS speaker at 10:55. Crisscross of new KFRS speaker at 10:55:30; still singing well. Another crisscross at 10:56. Another crisscross of KFRS speaker at 10:56:30. Back to midpoint at 10:57 at end of experiment; still singing well.

EXPERIMENT 3—same male, location, and date as above. Wild bird became silent at termination of last experiment; location now unknown. At 11:04 A.M. I began to walk around the experimental area, using playback of the Green Isolate at one year, to see if I could elicit a response. Played back for five minutes. Not until 11:08 did he sing at all, then only two renditions of song. The five minutes of playback ended with the wild bird silent.

EXPERIMENT 4—same male, location, and date as above. Wild bird still silent, location unknown at 11:10 when I began to repeat experiment 3, but using tape of the wild Wood Thrush (KFRS 1). The wild bird began to sing within 20 seconds, and continued to sing throughout the five minutes of playback; he followed me as I moved throughout his territory. Stopped singing when I discontinued playback at 11:15, and remained silent for the next 10 minutes while I packed my playback equipment.

SUMMARY: strong response to playback of songs of the wild Wood Thrush, including reorientation at the cable switch; no response to playback of the songs of the Green Isolate at one year of age.

On June 26, 1976, another Connetquot bird (CRSP 5) would not respond to playback of the songs of either isolate, and clearly discriminated between isolate song and the song of the wild Wood Thrush:

EXPERIMENT 15—Only one tape used: White isolate at two years (June 28). Only one speaker used. Had brought this wild bird into experimental area 15 minutes earlier with brief playback of song of a wild bird (KFRS 1), but bird was silent, location unknown at start of this experiment at 1:05 P.M. No show. No singing at all during five minutes of playback.

EXPERIMENT 16—same male, location, and date as above. Used same isolate tape as above; only one speaker used. Wild bird silent, location unknown at start at 1:12 P.M. No show. No singing during five minutes of playback.

EXPERIMENT 17—same male, location, and date as above. Tapes used: wild Wood Thrush (KFRS 1) vs. White isolate at two years (recording of June 28). Wild bird silent, location unknown at start at 1:18 P.M. Wild bird began singing within 45 seconds. Sang well and worked gradually closer to experimental area. Had reached edge of KFRS area by time of cable switch at 1:23. Still singing well. To midpoint by 1:27, singing well. Over to 30 ft. from new KFRS speaker by 1:27:30. Remained in vicinity of new KFRS speaker until end of experiment at 1:23.

EXPERIMENT 18—same male, location, and date as above. Now that the wild bird is within experimental area, I decided to repeat the last experiment, using the same tapes but reversing the speaker cables. Wild bird still at the same speaker (KFRS speaker of last experiment; isolate speaker at the beginning of this experiment) at start at 1:29 P.M., singing well. Moved to midpoint by 1:30. In to 40 ft. of new KFRS speaker by 1:31, singing well. Crisscross of new speaker at 1:33. Another crisscross. Cable switch at 1:34, with wild bird still in old KFRS area. Moved to midpoint by 1:36, still singing well. To within 20 ft. of new KFRS speaker at 1:38. Crisscross of new KFRS speaker at 1:39. Another crisscross just before end of experiment. Still in KFRS area, singing well.

SUMMARY: strong, consistent response to the songs of the wild Wood Thrush, including reorientation at the cable switch; no response to playback of the songs of White Isolate.

Another series of experiments, conducted on June 27, 1976, demonstrates the lack of response of still another Connetquot bird (CRSP 4) to the songs of both isolates:

EXPERIMENT 19—Only one tape used: Green Isolate at one year. Wild bird silent, location unknown at start at 10:14 A.M. Wild bird began singing about 10:15, outside experimental area. By 10:16:30 had moved to 50 ft. from the isolate speaker, but then stopped singing. Cable switch at 10:20. Wild bird disappeared. Heard a bird in the distance at 10:22. No show; no response.

EXPERIMENT 20—same male, location, and date as above. Only one tape used: White Isolate at two years (recording of June 10). Wild bird still silent, location unknown at start at 10:25 A.M. Wild bird sang briefly at 10:28 (two song renditions), then silent again. At 10:29, he gave two more song renditions from outside experimental area. Cable switch at 10:30. Wild bird gave an occasional song from outside experimental area during the last five minutes of playback. Flew through experimental area and beyond at 10:32, but silent. At 10:33, wild bird singing well outside experimental area.

EXPERIMENT 21—same male, location, and date as above. Only one tape used: White Isolate at two years (recording of June 28). Start at 10:35 A.M. Can hear the wild bird outside experimental area, but there was no orientation toward the speaker. At 10:37, wild bird singing at about midpoint, but then moved out of experimental area after one minute. Cable switch at 10:40. No singing at all during last five minutes of playback.

EXPERIMENT 22—same male, location, and date as above. Tapes used: wild Wood Thrush (KFRS 1) vs. White Isolate at two years (recording of June 28). Wild bird still silent, location unknown at start at 10:46 A.M. Wild bird started to sing within 10 seconds. Had moved to midpoint by 10:46:30. Moved into area of KFRS speaker by 10:48, with good sustained song. Singing from perch 15 feet from KFRS speaker. At 5 ft. from KFRS speaker at 10:50, singing well. Cable switch at 10:51. Reoriented to new KFRS speaker within one minute. Singing within 30 ft. of new KFRS speaker at 10:53. Remained in area of that speaker for remainder of experiment, singing well.

SUMMARY: strong, consistent response to the songs of the wild Wood Thrush, including reorientation at the cable switch; no response to playback of the songs of the Green Isolate and of the White Isolate.

DISCUSSION

At the onset of this study I posed the following question: will a Wood Thrush, handreared from the egg and isolated from experienced conspecifics for two years, develop a normal, species-characteristic primary song? I am impressed with the extent of the similarity between the songs of the isolates and those of wild Wood Thrushes, even though the isolates' songs developed over a period of nearly two years without exposure to experienced conspecifics. Spectrographic comparisons show similarities in basic structure, syntax, and rhythm of the songs, as well as in the use of two simultaneous signals with unrelated frequencies. In addition, the size of the repertoire of phrase types developed by each of the isolates was typical for the species, as was the frequency of use of these phrases and of the resulting patterns of song. That these characteristics are to be found in the songs of the Green Isolate at one year old, in the absence of any previous singing by the sibling isolate, suggests that this degree of similarity is not dependent upon auditory feedback or stimulation from other siblings. To the extent, then, that these parameters of isolate song reflect those of the song of wild Wood Thrushes, the primary song developed by the experimental isolates in this study is remarkably species-characteristic.

The only consistent differences between the spectrograms of the songs of the isolates and those of wild Wood Thrushes are in the central phrases, which are less musical, more discordant, simpler in configuration (less heterogeneous), and shorter in duration in isolate song. The nature of these differences, together with the fact that wild Wood Thrushes did not respond to playback of isolate song, suggest the possibility that the more intense, normally flutelike notes of the central phrase transmit information required for species-recognition. To the extent that there are these differences in the central phrases of isolate song and wild song, the primary song of the isolates is not species-characteristic and, more importantly, does not elicit response from wild Wood Thrushes. Further playback experiments are required, using songs in which the central phrases have been

experimentally altered or synthesized, to determine which of these differences relate to species-recognition.

A second question was asked: after exposure to an enriched auditory environment, including the frequent singing of a wild Wood Thrush on territory, will the experimental bird at nearly two years of age add to or modify its primary song? The changes effected in the songs of the Green Isolate, during its second year of isolation and after exposure to the songs of a wild Wood Thrush and of the sibling isolate, were those brought about by elimination of the experimentation that characterized this isolate's songs at the end of the first year. Phrase types remained constant from the first to the second year, however, and no new phrases were added to the repertoire. There were no improvements in the quality of the central phrases, i.e., changes that would have made them more species-characteristic, for they failed once again to elicit a normal response from wild Wood Thrushes. This evidence discounts any influence of tutors during the second year.

The fact that the White Isolate did not develop imitations of the patterns of central and terminal phrases in Green's repertoire, even though they were housed together during the entire period of song development, is evidence that the gross patterns of phrases, *per se*, are not learned from conspecifics. This would appear to explain the great variety of phrase types to be found within and among the individual repertoires of Wood Thrushes, a fact that has led to the observation (Saunders, 1924; Borror and Reese, 1956; Borror, 1961; this study) that individual Wood Thrushes can be identified unerringly by their central and terminal phrases.

Since the White Isolate did not modify its central phrases after exposure to the wild Wood Thrush at two years of age, we can hypothesize that he was no longer receptive to tutors at that stage. This modification of the central phrases, through learning from experienced conspecifics, probably takes place during the juvenile's first summer and fall. In White's case, song development was delayed, presumably due to dominance by Green, and it is difficult to delimit this period of receptivity to tutors, other than that it must have ended prior to its second May.

In planning for future research on the development of song in the Wood Thrush, the following points should be considered: (1) isolates, deprived of exposure to experienced conspecifics during their first 10 months, can be expected to develop song that is remarkably species-specific, but lacking in certain characteristics of the central phrases that transmit information required for species-recognition; (2) the period of receptivity to experienced conspecifics, during which the central phrases become modified through learning, probably coincides with the first four months and does not extend beyond the tenth month of age; (3) the characteristics of the central phrase that contain information relating to species-recognition may include, among others, degree of heterogeneity, musical quality, and duration of the notes, and should be altered or synthesized experimentally to determine their relative importance in eliciting normal response from wild birds; (4) the bioassay of the message content of experimentally altered central phrases will require carefully-controlled playback experiments that provide for quantified responses of the wild birds.

APPENDIX

Data for Sound Recordings Used for the Spectrograms Figured in this Report

Figure	Individual	Locality	Date	Catalogue Number
4:1	CRSP No. 4	Connetquot River State Park, Islip, New York	June 26, 1976	195A1-726
4:2	CRSP No. 2	Connetquot River State Park, Islip, New York	June 25, 1976	195A1-306

Figure	Individual	Locality	Date	Catalogue Number
4:3	CRSP No. 5	Connetquot River State Park, Islip, New York	June 26, 1976	195B4-109
4:4	CRSP No. 3	Connetquot River State Park, Islip, New York	June 25, 1976	195A1-542
4:5	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-181
4:6	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-011
4:7	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-585
6:1	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-265
6:2	Green Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	May 28, 1976	193B3-290
6:3	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-285
6:4	Green Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	May 28, 1976	193B3-283
6:5	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-011
6:6	Green Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	May 28, 1976	193B3-286
6:7	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-165
6:8	Green Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	May 28, 1976	193B3-281
7:1	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-159
7:2	Green Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	May 28, 1976	193B3-294
7:3	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-199
7:4	Green Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	May 28, 1976	193B3-298
7:5	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-205
7:6	Green Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	May 28, 1976	193B3-302
7:7	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-191
7:8	Green Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	May 28, 1976	193B3-296
8:1	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-241
8:2	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-027
8:3	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-029
8:4	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-233
8:5	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-014

Figure	Individual	Locality	Date	Catalogue Number
8:6	Green Isolate, first year	Kalbfleisch Field Research Station; isolation chamber	May 18, 1975	190B3-298
8:7	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-621
8:8	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-639
8:9	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-598
9:1	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-287
9:2	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-269
9:3	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-278
9:4	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-240
9:5	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-268
9:6	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-241
9:7	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-245
9:8	KFRS No. 2	Kalbfleisch Field Research Station, Huntington, New York	June 26, 1976	195B4-267
10:1	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-585
10:2	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-640
10:3	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-632
10:4	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-592
10:5	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-644
10:6	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-628
10:7	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-596
10:8	White Isolate, second year	Kalbfleisch Field Research Station; outdoor aviary	June 28, 1976	195B4-646

LITERATURE CITED

Borror, D. J.
1961. Intraspecific variation in passerine bird songs. Wilson Bull., vol. 73, pp. 57-78.

Borror, D. J., and C. R. Reese
1956. Vocal gymnastics in Wood Thrush songs. Ohio Jour. Sci., vol. 56, pp. 177-182.

Ewert, D. N.
1978. Song in the Rufous-sided Towhee (*Pipilo erythrophthalmus*). Ph.D. Dissertation, The City Univ., New York.

Gottlieb, G.
1968. Prenatal behavior of birds. Quart. Rev. of Biol., vol. 43, pp. 148-174.

Gottlieb, G., and J. G. Vandenbergh
1968. Ontogeny of vocalizations in duck and chick embryos. Jour. Exp. Zool., vol. 168, pp. 307-325.

Greenewalt, C. H.
1968. Bird song: acoustics and physiology. Smithsonian Inst. Press, Washington, D.C., 194 pp.

Konishi, M., and F. Nottebohm
1969. Experimental studies in the ontogeny of avian vocalizations. *In* Hinde, R. A. (ed.), Bird vocalizations. Cambridge Univ. Press, pp. 29-48.

Lanyon, W. E.
1960. The ontogeny of vocalizations in birds. *In* Lanyon, W. E., and W. N. Tavolga (eds.), Animal sounds and communication. Publ. Amer. Inst. Biol. Sci., no. 7, pp. 321-347.
1963. Experiments on species discrimination in *Myiarchus* flycatchers. Amer. Mus. Novitates, no. 2126, 16 pp.
1967. Revision and probable evolution of the *Myiarchus* flycatchers of the West Indies. Bull. Amer. Mus. Nat. Hist., vol. 136, pp. 329-370.
1978. Revision of the *Myiarchus* flycatchers of South America. *Ibid.*, vol. 161, pp. 427-628.

Lanyon, W. E., and V. H. Lanyon
1969. A technique for rearing passerine birds from the egg. The Living Bird, Eighth Annual, Cornell Lab. of Ornith., Ithaca, New York, pp. 81-93.
1971. A technique for rearing passerine birds from the egg. Revised and amended. Avicultural Bull., May 1971, pp. 11-33.

Marler, P.
1964. Inheritance and learning in the development of animal vocalizations. *In* Busnel, R. G. (ed.), Acoustic behavior of animals. Amsterdam, Elsevier, pp. 228-243.

Marler, P., and S. Peters
1977. Selective vocal learning in a sparrow. Science, vol. 198, pp. 519-521.

Messmer, E., and I. Messmer
1956. Die Entwicklung der Lautäusserungen und einiger Verhaltensweisen der Amsel (*Turdus merula merula* L.) unter natürlichen Bedingungen und nach Einzelaufzucht in schalldichten Räumen. Z. Tierpsychol., vol. 13, pp. 341-441.

Nottebohm, F.
1970. Ontogeny of bird song. Science, vol. 167, pp. 950-956.
1975. Vocal behavior in birds. *In* Farner, D. S. and J. R. King (eds.), Avian Biology. New York Academic Press, vol. 5, pp. 287-332.

Saunders, A. A.
1924. Recognizing individual birds by song. Auk, vol. 41, pp. 242-259.

Shiovitz, K. A.
1975. The process of species-specific song recognition by the Indigo Bunting, *Passerina cyanea*, and its relationship to the organization of avian acoustical behavior. Behaviour, vol. 55, pp. 128-179.

Thielcke, G.
1973. Uniformierung des Gesangs der Tannenmeise (*Parus ater*) durch Lernen. Journal für Ornithologie, vol. 114, pp. 443-454.

Thielcke-Poltz, H., and G. Thielcke
1960. Akustisches Lernen verschieden alter Schallisolierter Amseln (*Turdus merula* L.) und die Entwicklung erlernter Motive ohne und mit künstlichen Einfluss von Testosteron. Z. Tierpsychol., vol. 17, pp. 211-244.

Vince, M. A.
1969. Embryonic communication, respiration and the synchronization of hatching. *In* Hinde, R. A. (ed.), Bird vocalizations. Cambridge Univ. Press, pp. 233-260.