

# SONG GROUPS IN A SINGING ASSEMBLY OF LITTLE HERMITS

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Displaying Little Hermits (*Phaethornis longuemareus*, Trochilidae) cluster year after year in particular areas of forest rather than dispersing throughout the habitat, and their singing continues throughout most of the day and year (Skutch 1951, 1954; Arp 1957; Snow 1968). To this extent, their singing assemblies resemble the leks, or communal display grounds, of some other birds in Neotropical forests. However, the Little Hermit differs from the well-studied, lek-forming manakins (Pipridae) (Sick 1967; Snow 1962a, b; Chapman 1935) and Cock-of-the-rock (*Rupicola rupicola*, Rupicolidae) (Gilliard 1962), in two important respects. First, a feature shared by all *Phaethornis* hummingbirds is the relatively slight sexual dimorphism in coloration and size. The sexes of the Little Hermit are apparently indistinguishable in the field. If the hermits have leks, they constitute an exception to the long-recognized correlation between considerable sexual dimorphism and promiscuous mating habits, which characterize lek-forming species (Darwin 1871; Sibley 1957). Three displaying Little Hermits collected at one singing assembly were all males (Arp 1957), so the persistently displaying birds at an assembly are probably males.

A second peculiarity of Little Hermits is the presence of song groups within their singing assemblies. Snow (1968), who first recognized this phenomenon, described neighboring males with similar songs which differed from the songs of other groups of males in the same singing assembly. Furthermore, the songs at most of the singing perches in one assembly appeared to remain constant in the course of three years, suggesting either that individual males retain the same perches from year to year and enjoy relatively high survival rates, or that the males succeeding each other at one singing perch tend to have similar songs.

In order to compare all the song groups in one singing assembly of Little Hermits, I studied an assembly in the Arima Valley, Trinidad, from 21 January to 3 February 1969 during the peak of the species' nesting season (Snow and Snow 1964). I mapped the singing perches and recorded the songs of almost all the birds at this assembly.

## PROCEDURES

Each perch on which a bird sang was marked with a 5-cm ribbon of orange flagging tape fastened to the twig about 0.2–0.5 m from the actual spot used by the singer. The birds usually returned to these marked perches within a minute or so. In no case did I find any indication that the nearby orange tape disturbed the birds. Once the perch was marked in this way, I could on subsequent visits quickly locate it from a distance and observe the bird's behavior.

Recordings were made with a Nagra III PHO tape recorder and a Sennheiser MKH 804 directional, condenser microphone. Songs were analyzed on a Kay 6061-B Sound Spectrograph with the wide band-pass filter (effective resolution, 600 Hz). In analyzing the songs recorded at each site, I tried to examine all possible sources of variation. Songs were chosen as widely separated in time as possible, from different sections of singing bouts, or simply whenever they sounded different. Echoes from the high-pitched songs sometimes created difficulties in interpreting the fine structures and durations of the notes. Unusually careful examination and comparison of the spectrograms became necessary in these cases.

To study bouts of song, I recorded longer sequences (about 30 min) on a Uher 4400 Report Stereo tape recorder at a tape speed of 3¾ ips using a Uher microphone and a parabola 2 ft in diameter. These sequences were analyzed by recording the amplified output of a Hewlett-Packard 500B Frequency Meter on a Sanborn 151 Recorder. The records allowed me to correlate some features of each song with the length of the pause preceding it.

Using compass and range-finder, I prepared a map of the area occupied by the hummingbirds. I used the range-finder to measure directly the distances between neighboring singing perches whenever the vegetation permitted an unobstructed sighting.

## DESCRIPTION OF SINGING ASSEMBLY AND SONG PERCHES

The area I studied extended up a south-facing slope at Mile 7¼ on the Arima Valley Road, several miles from the singing assemblies studied by Snow (1968). At an elevation of 1050–1150 ft (320–350 m) this area supported a mature forest with a structure resembling Beard's (1955) description of Lower Montane Forest. Large trees formed a nearly continuous canopy about 27–30 m above ground.

Each singer chose a slender (1.5–4 mm in diameter), roughly horizontal twig, usually within or beside a pile of twigs and branches on the forest floor. Nineteen regularly occupied singing perches which I measured were, on the average, 33.3 cm above ground

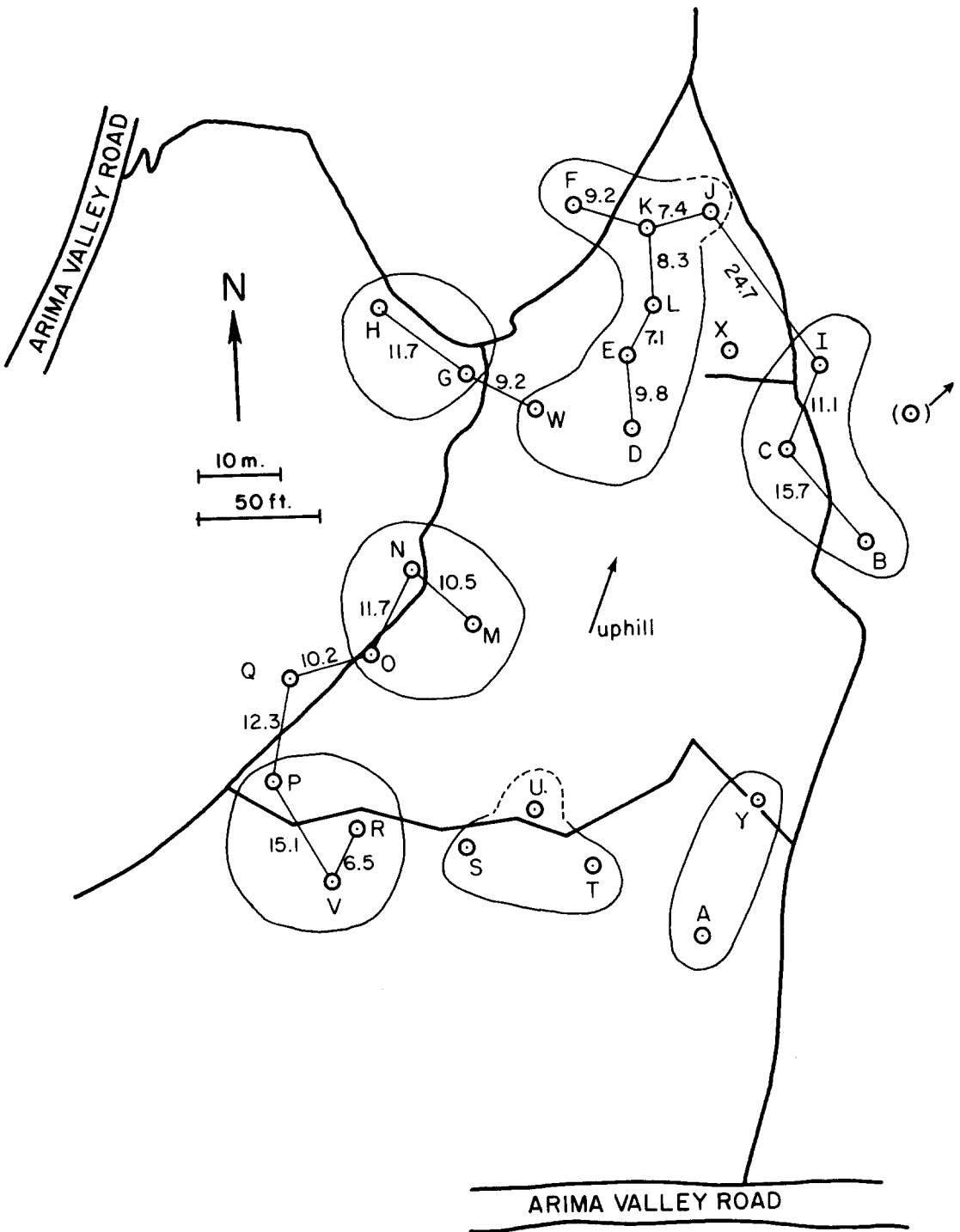


FIGURE 1. Regular singing perches and song groups. Small circles indicate positions of regular singing perches. Straight lines join those perches whose separation I could measure directly with a range finder, and the distances are indicated in meters. Curving lines enclose sites belonging to the same song group. No recordings were made at Sites J and U; they are tentatively included in the same song groups as the sites nearest them. The heavy lines are foot trails.

(range, 22–45 cm). One other was much higher (58 cm). The singing perches were thus well concealed in the deep shade near the forest floor.

The singers occupied their perches with remarkable regularity. Day after day birds sang not only from the same twig but from the same position on the twig. Such a con-

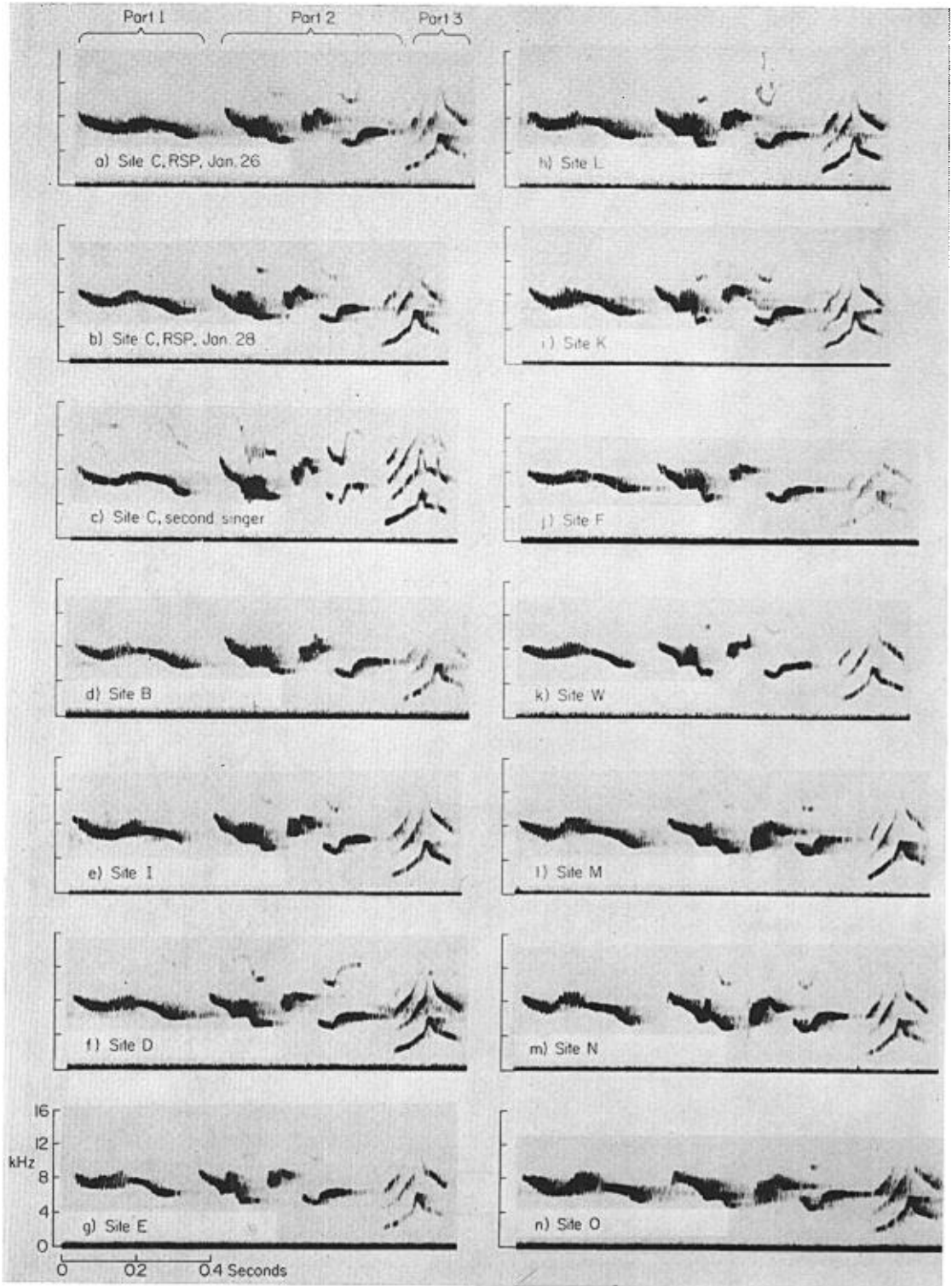


FIGURE 2. Spectrograms of songs recorded at 22 perches. Effective resolution of the filter: 600 Hz.

stantly used perch I shall call a regular singing perch (RSP). Auxiliary perches were used only when I was very near a singing bird, or when two birds sang within 2–4 m of each

other. On a number of occasions, when first locating a singer's perch, I had to approach so close that the bird shifted among three or four perches. Invariably when I marked all

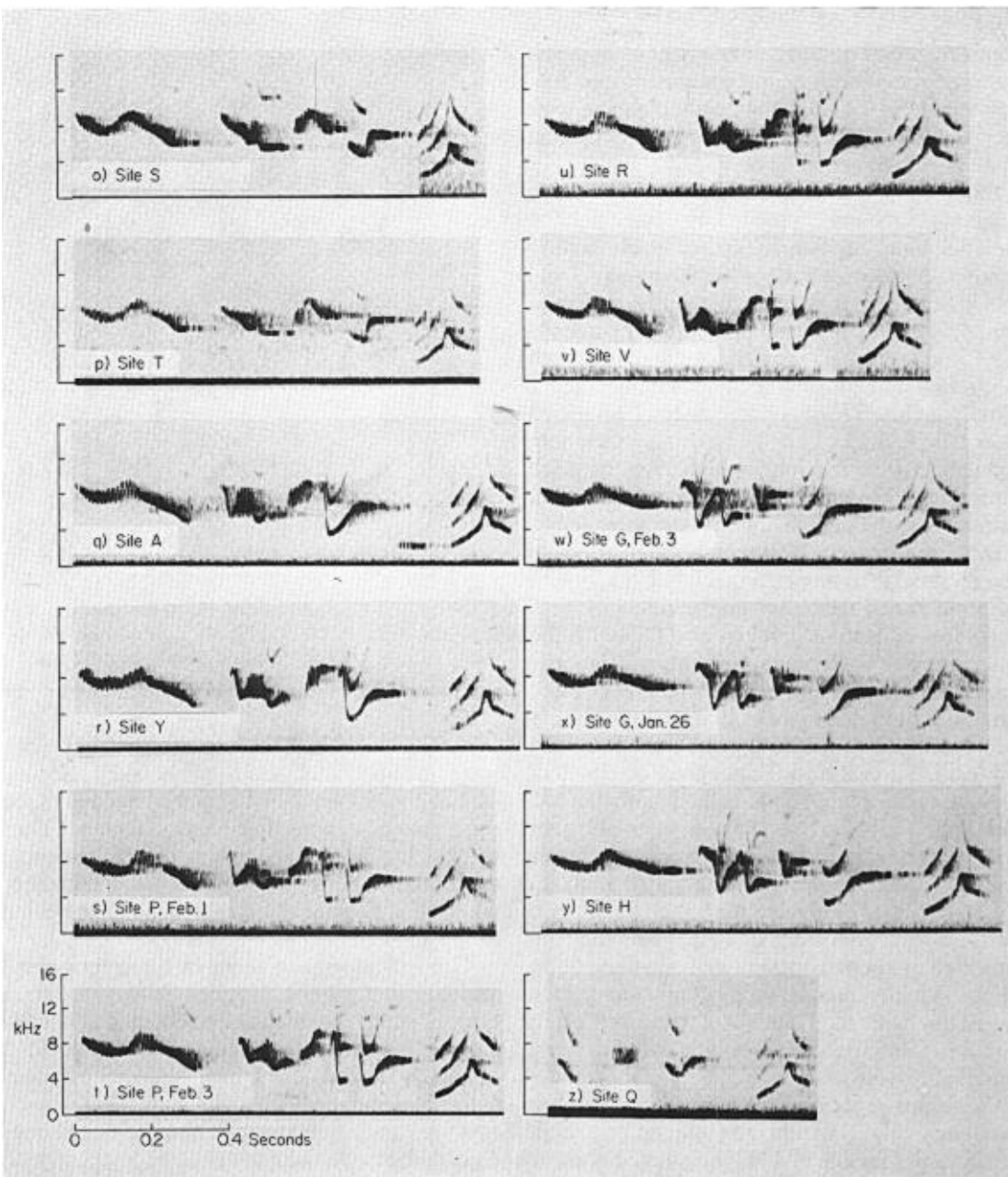


FIGURE 2. Continued.

these perches and then subsequently observed from 10 m or farther away, I found the singer using only one. On several occasions when two birds sang near each other, one bird would occupy the RSP between chases while the other would sing from a perch nearby. In one unique situation at site C (described below), two birds sang together regularly.

Figure 1 represents the arrangement of RSP's within the singing assembly. The assembly satisfied one criterion of a lek: the displaying birds clustered within a part of the

available habitat. The assembly did not extend farther uphill than sites J, K, and F, although the forest continued without apparent change and unoccupied fallen branches were available. No other singers resided to the south or west of those shown. In both these directions the Arima Valley Road borders the study area. I traversed the large gap in the center of the assembly several times without finding singing birds. Here the habitat may have been unsuitable, since no tangles of dead branches and twigs were present.

## DESCRIPTION OF SONGS

Songs recorded on different days at each perch showed remarkable constancy in their fine structure (fig. 2a, b, s, t, w, x), which suggests that the same individual returned to sing at each perch on successive days.

Each song consists of three parts distinguished by Snow (1968) (fig. 2a). Part 1 includes one or two whistles, each lasting about 0.3 sec and falling in frequency from 8–9 kHz to about 6 kHz. Near the middle a temporary rise in mean pitch accompanies a very rapid warble, which may include both frequency and amplitude modulation. Part 2 usually includes three or four notes (described in detail below). Part 3 consists of one note about 0.15–0.19 sec long which rises in pitch from about 2 to nearly 6 kHz, then falls again. Harmonics are prominent in this note.

In choosing songs for analysis, I tried to reveal any differences correlated (1) with different songs from any one perch, (2) with songs from different perches, and (3) with the song groups. Variation among songs from any one perch seemed limited to three types. First, Part I might include one or two whistles, rarely three, and exceptionally more than three. In any case, Parts 2 and 3 appeared unaffected. Second, incomplete songs lacked both Parts 2 and 3 or only Part 3. Part 2, consisting of three or four rapid notes, was essentially never broken in the middle. Most individuals in my study area rarely omitted Part 3. At two sites, however, omission of Part 3 was the rule rather than the exception, as I shall mention below. Finally, among songs at any one perch, the notes in Parts 1 and 3 of the song often varied in minor details, although Part 2 showed remarkable constancy.

Variations specific to individual perches were very slight within any one song group. At some perches Part 1 of the song did show slight but constant individual peculiarities. For instance, at Site S, the first half of the whistle consistently showed a large drop in pitch (fig. 2o). By contrast, Part 3, which varied considerably from song to song at each perch, showed no constant differences from perch to perch within song groups. Part 2 was remarkably constant within each song group.

Characteristics of the song groups were especially prominent in Part 2 of the song. The following section will describe these characteristics in detail.

## SONG GROUPS

Two features of the songs of Little Hermits stand out in the following discussion. First,

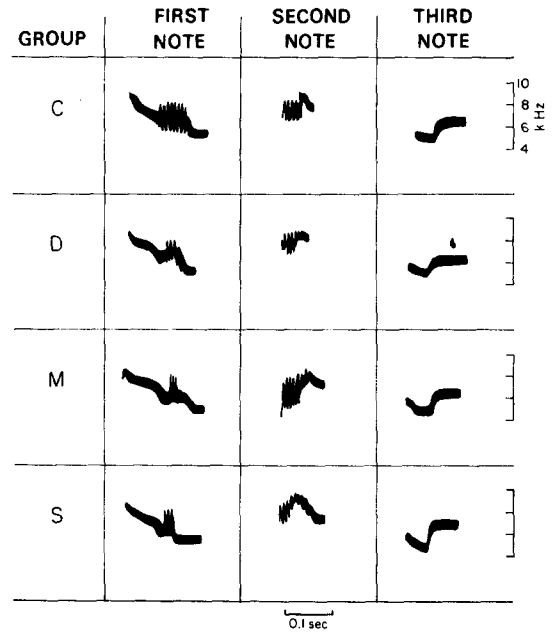


FIGURE 3. Comparisons of the three notes in Part 2 of the song in the C, D, M, and S song groups. Each note is traced from a typical spectrogram.

the songs at neighboring sites within each song group match each other very closely, especially in Part 2 of the song. Second, such song groups vary in their distinctiveness. Thus the C-, D-, M-, and S-groups closely resemble each other (fig. 3), as do the A- and P-groups, while the G-group resembles no other song group closely.

The spatial arrangement of the song groups appears in figure 1. Figure 2a–z presents a typical song recorded at each of 22 regular singing perches (all of the perches I located except J, U, and X). I have verified all characteristics mentioned in the following discussion by examining spectrograms of 5–15 songs recorded at each site.

*Sites C, B, and I* (C-group) (fig. 2a–e). Site C was unique among those I studied since two birds frequently sang near each other on different perches. One bird usually sang from the RSP, the most persistently occupied perch, but occasionally I saw this bird fly to a perch 1.5 m SSE and sing there. The second singer used a number of perches within 3 m of the RSP, but most frequently sang from a perch 2.5 m ENE of the RSP. The two birds differed slightly but consistently in the timbre of their songs. The first note of Part 2 sounded noticeably harsher in the second bird's songs. When two singers were present, the bird on the RSP frequently interrupted its singing to chase the second bird

for as long as 30 sec at a time. When only one singer was present, it was the one on the RSP. The constancy with which the characteristics of songs and behavior correlated with the different perches suggests that the same two individuals were present every day.

Sound spectrograms of songs recorded from the bird associated with the RSP at site C are all very similar. Part 2 consists of three notes ranging in pitch from 5 to nearly 9 kHz and lasting slightly more than 0.4 sec. The first note falls in pitch except when interrupted by rapid warbling for 0.04 sec. The second note begins with rapid warbling, then quickly rises and falls. The third note consists of a 0.05-sec whistle at about 5 kHz, followed by an equally long whistle at 6.3 kHz. The second bird at C, with a harsher first note in Part 2, differs in that the warble in this note extends over a slightly wider frequency range. The second note also rises to a higher pitch.

Songs from sites I and B resemble those from the RSP at C very closely. All four birds (C-RSP, C-2, B, and I) were often heard singing simultaneously.

*Sites D, E, L, K, F, and W* (D-group) (fig. 2f-k). These songs show basic resemblances to those of C-group, but constant differences in Part 2 include the following: (1) the warble is preceded and followed by sharp dips in pitch in the first note; (2) no final drop in pitch in the second note; and (3) a slightly longer whistle at the end of the third note. Songs from sites E, L, K, and F are virtually indistinguishable from those from D. Songs from W sometimes show slight modifications.

*Sites M, N, and O* (M-group) (fig. 2l-n). These resemble the preceding. The second note of Part 2, however, begins with a warble extending over a much wider frequency range and ends with a sharp fall in pitch. The initial whistle of the third note also falls in pitch. Songs from M, N, and O are all closely similar. Songs from M and N agree also in a peculiarity in Part 1; when two whistles occur, the second is abbreviated by stopping with the warble which otherwise would come in the middle of the note.

*Sites S and T* (S-group) (fig. 2o, p). Here a combination of previously described features occurs. The first note of Part 2 resembles those of D and M. The second note ends with an even more exaggerated downward slur than that of M. The third note begins as in M but then rises abruptly to a slightly higher pitch for the final whistle (6.8 kHz compared with 6.4 kHz for M and N, and 6.0-6.2 kHz for D, E, etc.).

*Sites A and Y* (A-group) (fig. 2q, r). A strikingly different pattern appears here. Especially notice (1) the rapid downward sweep in frequency which starts the first note in Part 2, (2) the second note which consists of a warble rising in mean pitch, and (3) the exceedingly rapid sweep through nearly 6 kHz which initiates the third note. Songs from sites A and Y agree closely in structure. Both omit Part 3 much more often than they include it, a striking difference in comparison with all other sites.

*Sites P, R, and V* (P-group) (fig. 2s-v). Here the resemblance to A and Y is strong. A constant difference is the doubling of the frequency sweep which begins the third note in Part 2. Also, the warbles in the first and especially the second notes are not so pronounced. Finally these birds do not share the tendency of A and Y to omit Part 3.

*Sites G and H* (G-group) (fig. 2w-y). A third radically different type is characterized by wholly new patterns in the first and second notes of Part 2. The birds at these two sites, unlike the birds in all other song groups, agree in never singing songs with two whistles in Part 1.

*Site Q*. (fig. 2z). The bird at this site, present as consistently as its neighbors, sang a soft, incomplete version of a normal song. Part 3 is recognizable, as is the third note of Part 2, which closely matches those of M, N, and O, his closest neighbors. The two notes beginning his song may represent precursors of the first and second notes in Part 2. No suggestion of Part 1 is present. Perhaps this site belonged to a young bird in the process of acquiring a mature song pattern.

#### PATTERNING OF SONG BOUTS

Typically a bird alternated 10-15 min of singing from its perch with 2-3-min absences. Within a singing period, songs were usually arranged in bouts of rapid singing separated by pauses. The two birds at site C sang in short bouts in which the first song began with one whistle in Part 1 (One-whistle Songs) and all subsequent songs began with two whistles (Two-whistle Songs). Two whistles occurred only if the pause preceding the song was very short (less than 0.3 sec), that is, within rapid bouts. At site B, however, Two-whistle Songs were much less common and regularly began singing bouts after long pauses. Also, the variance of intervals preceding One-whistle Songs was greater. The similarities between neighboring sites within the same song group thus did not always include

the patterning of song bouts. At sites G and H Two-whistle Songs were never recorded.

## DISCUSSION

Evidence that only one bird used each regular singing perch included the constancy of the song pattern and the attendance at each perch. Since no evidence contradicted this hypothesis, I have tentatively concluded that one bird sang regularly at each RSP.

## FUNCTIONS OF THE COMPLEX SONG

The elaborately patterned songs of Little Hermits are exceptional among songs of hummingbirds. This elaboration of acoustic characteristics might relate to the visual drabness and sexual monomorphism of the species. Since the birds display in the gloom of dense undergrowth within forests, the elaborate songs could function in place of conspicuous plumages in intraspecific communication at long distances (Hartshorne 1958). Only when two Little Hermits interact at close range (1 m  $\pm$ ) do displays with conspicuous visual components occur (Skutch 1951, 1964; Arp 1957; Snow 1968; pers. observ.). However, the elaborate songs of Little Hermits might also relate to the presence of dialects, since their complex songs could allow clear differentiation of song groups. In general, more complex songs could furnish more information and allow more distinctions among groups or individuals.

## FORMATION OF THE SONG GROUPS

My observations of Little Hermits confirm Snow's (1968) conclusion that the song groups usually coincide with spatial groupings of the singing perches. The strict homogeneity of neighboring birds' songs within any one song group strongly suggests that either an individual obtains a singing perch and then imitates the dialect characteristics of its neighbors' song or, after acquiring a song pattern, each individual tends to choose its perch near the area in which it learned the characteristics of its song. Two observations suggest that at least some male Little Hermits did acquire their song patterns before settling at their present singing perches. First, G and W are clear examples of birds that do not sing the song pattern of their nearest neighbor. A second line of evidence involves the similarities among different song groups. I have described how the seven song groups partition easily into three classes. The C-, D-, M-, and S-groups are clearly related, as are the P- and A-groups. Indeed, the M- and S-groups share

more similarities in Part 2 of their songs than either shares with the D-group, and all three of these share similarities not present in the C-group (fig. 3). These relationships, together with the spatial relationships of the groups, suggest that the song groups might have developed by fixation of the variant song patterns of founder individuals. Thus a bird with a minor variant of the D-group song could have moved away from the D-group and formed the nucleus for the C-group. A bird with another variant of the D-group song could have started the M-group, and a bird with a variant of the M-group song could have founded the S-group. Each song group would grow as additional birds imitated the variant song and settled nearby. The relationships between the P- and A-groups are clearly analogous to the relationships among the C-, D-, M-, and S-groups. The possibility that spatially intermediate song perches once linked the C-, D-, M-, and S-groups, as well as the A- and P-groups, could also explain the spatial arrangement of the song groups. The location of the S-group directly between the A- and P-groups, however, creates difficulties in defending this hypothesis. Thus each song dialect might have arisen around a founding individual with an imperfect imitation of a previously existing song pattern.

## LACK OF INDIVIDUALITY IN SONGS

Bird songs often include characteristics specific to different individuals (Marler 1960). In some species, individual recognition by vocal characteristics is important for the maintenance of pair-bonds and for habituation of aggressive responses to males established on neighboring territories (Weeden and Falls 1959; Falls 1969).

However, the songs of Little Hermits within any one song group usually lack characteristics specific to the individuals. As in the White-crowned Sparrow (*Zonotrichia leucophrys*), this minimizing of differences among neighboring individuals produces homogeneous dialects (Marler and Tamura 1962). Presumably the virtual absence of individual characteristics in Little Hermits' songs should hinder individual recognition between sexual partners or among neighbors in the singing assembly. However, if each bird strictly confines its singing to one small area, usually to one perch, this localization could provide highly individual identification for each singer. Indeed, persistent singing at a new site elicited clear reactions from neighboring singers. On the final day of my study a bird sang repeatedly

at site X (fig. 1), where singing had never been heard before. Several times the singer on the RSP at site C and the singer at site I left their perches and flew toward X. In addition, playbacks of tape-recorded songs quickly stimulated nearby singers to approach the loudspeaker, regardless of which dialect I had broadcast. Thus strict localization might provide the clue to a singer's identity.

Since the patterning of song bouts at sites C and B differed so clearly, these patterns could also form a basis for individual recognition of the singers within a song group. I obtained long recordings of song bouts only at sites C, B, and G. However, less systematic observations suggested that song bout patterns were usually similar at all sites within a song group. For instance, at all sites in the C- and D-groups, except at site B, song bout patterns resembled the patterns recorded at site C. Individual differences in the patterning of song bouts need further study.

To assess how song groups might relate to mating patterns in singing assemblies of Little Hermits, one would eventually like to know whether individual females in their successive matings remain faithful to a particular dialect more than to a particular male within that dialect, and also whether dialects with more numerous members accomplish disproportionately more matings than do ones with fewer singers.

## SUMMARY

At one singing assembly of Little Hermits in Trinidad, I tape-recorded the songs of almost every bird that occupied a regular singing perch. The songs were analyzed on a sound spectrograph. My results confirm and extend Snow's (1968) report. Apparently only one individual sang regularly on each perch, since songs recorded on different days at the same perch were invariably the same. Each of 23 singers belonged to one of seven song groups which, with one exception, paralleled the spatial groupings of the singing perches. The song groups were remarkable for their small size, internal homogeneity, and discrete separation. The differing degrees of similarity among the song patterns of different groups suggest that each group might have arisen around a founding individual with an imperfect imitation of a previously existing song pattern. The elaborate songs of Little Hermits, unusual among hummingbirds, perhaps evolved both because the birds display in dark sites, unsuitable for visual display, and to allow the differentiation of song dialects.

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