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THE SINGING ASSEMBLIES OF LITTLE HERMITS

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In forest hummingbirds of the genus *Phaethornis* a well known but nonetheless puzzling feature of behavior is the singing assemblies of males. Brewster and Chapman (1895) described the singing assemblies in the Green Hermit (*P. guy*), Davis (1934) in the Reddish Hermit (*P. ruber*), and Nicholson (1931) and Davis (1934) in the Long-tailed Hermit (*P. superciliosus*), while Skutch (1951) and Arp (1957) gave detailed accounts of this behavior in the Little Hermit (*P. longuemareus*). This paper, based on observations that Mrs. Snow and I made on Little Hermits in the Northern Range of Trinidad from 1956 to 1963, mainly in 1959-1961, is concerned primarily with the song of this very small hummingbird.

I do not claim in this paper to clarify the function of the assemblies any more than have the authors of earlier papers. The behavior has puzzled all observers, partly because of the extremely rapid movements of the birds and partly because the sexes are hardly distinguishable in the field. Birds collected at the assemblies have on examination all turned out to be males. Thus the assumption, which I believe correct, is that the singing assemblies are "leks," comprised of males, which the females visit for mating. A somewhat parallel behavior occurs in manakins (Pipridae)—see, for example, the recent review of the subject by Sick (1967).

The Little Hermit is extremely small, even for a hummingbird. Its weight averages just over three grams. Like other members of its genus it is rather dull-colored—brownish above and buff below, with a dark eye-stripe and blackish throat. The long central tail-feathers are tipped with white. The long, decurved bill is dark except for the basal part of the lower mandible and the gape which are yellow (Plate I).

Little Hermits are more abundant than any other hummingbird throughout much of the Trinidad forest. They spend most of their time inside the forest or along the edges, within a few feet of the ground, sucking nectar from the flowers of a large variety of herbs, shrubs, trees, vines, and epiphytes, as well as taking insect food. In spite of their abundance they are so inconspicuous and their movements are so quick that one rarely has an opportunity to watch one for long, except at the leks or singing grounds. In common with other hummingbirds in Trinidad, they breed from December to June—that is, from about a month before the dry season begins until about a month after it ends (Snow and Snow, 1964). The nest, suspended in the fashion typical of hermits from the tip of a leaf or fern frond, usually is very difficult to see. In spite of the birds' abundance we found only eight occupied nests in the course of over four years' field work. It seems very probable, though critical observations are lacking, that only the female is associated with the nest (Skutch, 1951).

The Singing Grounds

My first experience with a singing assembly of Little Hermits was on 25 February 1956, at about 2,300 feet up on a ridge of the Northern Range of Trinidad. In a part of the forest where the undergrowth was rather thick and tangled, I found myself surrounded by the sound of many squeaky, chattering songs which seemed to rise from the ground all around me. With a little patience I discovered that these songs came from a group of Little Hermits, each of which was perched in the undergrowth about a foot above the ground and about ten yards or so from its nearest neighbors. The whole assemblage occupied an area of perhaps 100 by 30 yards. In spite of the poor light, the twiggy undergrowth, and the minute size of the birds the singers betrayed themselves in the end by a continuous up and down wagging of their white-tipped tails.

Later, I found that in hilly country the singing grounds of the Little Hermit are usually on a ridge, similar to the one where I had my first experience, and that in parts of the Northern Range where the birds are very common, the singing assemblies may be almost continuous for considerable distances. Indeed, one may walk for hundreds of yards along the main ridge without being out of earshot of the songs of these little birds. Flat country suits them too. I found singing assemblies in an absolutely level, swampy forest near the eastern side of the island. And in every situation, no matter where it is, a certain amount of twiggy undergrowth is necessary to provide perches and cover for the singing birds. Arp (1957) suggested, from his observations, that singing grounds have to be on south-facing slopes, since song and display apparently depend on a certain level of illumination. Though I did not study this point, the main singing grounds which I observed were in fact on slopes which faced predominantly south.

The singing grounds are traditional, and there is every reason to believe that they persist indefinitely as long as the forest is suitable. One assemblage, on a steep ridge behind our house in the Arima Valley, was occupied in 1957, the year I first climbed the ridge. It was still occupied in 1963; and at least from 1959, when we began our detailed observations, onwards, the same perches were occupied year after year. I never had any evidence of a singing assembly changing its site.

The Daily and Seasonal Pattern of Activity

As I have mentioned already, the Little Hermits in the Northern Range of Trinidad breed from December to June. During the period of post-breeding molt — from July to September — they cease singing and displaying. The singing grounds are deserted. The birds begin to re-occupy the grounds in November, and by the end of the month or by early December most of the old birds are back at their perches. There they maintain their activity, with no marked fluctuations, until the following June. Activity declines in July, when most of the adults come into molt, and has practically ceased by the end of the month.

On several occasions I saw new, unestablished birds appear at the singing assemblies about April, and I assumed that these were young birds of the previous breeding season. A few other newcomers appeared in June and July, right at the end of the season. Their songs were rather undeveloped and I therefore surmised that they were young, possibly six months old, from the early nestings of that season.



Plate I. A Little Hermit feeding at the flower of an introduced tree, the Pride of Burma (*Amherstia nobilis*), in the Arima Valley, Trinidad. Photograph by B. Brower Hall.

Throughout the singing season, each individual is on its perch for the greater part of the day. Our hour-long watches at a number of song perches between 0700 and 0900 showed that at this time of day the birds were present from 67 to 92 per cent of the time.

We maintained a continuous watch on the perch of one individual from the time it arrived in the morning at 0641 until it left in the late afternoon at 1717. The bird left its perch 48 times that day. Twenty-two of its absences lasted under two minutes, and only five of them lasted over eight minutes. The bird sat on its perch a total of 444 minutes, or 70 per cent of the time, and the length of periods when it was on its perch averaged about nine minutes.

The birds sing more or less without a break all the time they are on their perches, at the rate of about 30 songs per minute. The maximum recorded was 32 per minute. Thus the singing is divided into a number of song-bouts, corresponding to the periods when the bird is present. Typically, at the beginning of a song-bout the songs are uttered in rapid succession, and towards the end of the bout the frequency falls off a little and the songs may be incomplete. The bird becomes restless; it may stretch and gape; and eventually, often after a short aerial display, it flies off.

The output of song is remarkable. The particular bird which we watched all day sang for approximately 400 of the 444 minutes it was on the perch. Our large number of counts revealed that the songs were uttered at an average rate of one every two seconds, a total of about 12,000 songs in a day. And we had no reason to suppose that this individual was any more persistent than the other singers.

Song Variation

The song is a brief, high-pitched, chattering phrase, usually lasting from 1 to 1.5 seconds, with a fundamental frequency mainly between 5,000 and 9,000 cycles per second (Figures 1 and 2). To my ear a typical utterance sounds something like *ee-wee tiddly weet*, and this three-part rendering, though far from perfect, brings out some of the main characteristics of the song-type prevalent in Little Hermits in the Arima Valley of Trinidad. These characteristics are as follows: In Part 1, one or two introductory notes (the *ee-wee*), longer than any other notes of the song, showing in spectrograms as a U-shaped section followed by a downward slur. In Part 2, a complex central phrase (the *tiddly*), rather variable but, when well developed as in Males K and P in Figure 1, showing a succession of extremely rapid changes of pitch. In Part 3, a terminal, lower-pitched note (the *weet*), occasionally repeated, rising and falling sharply in pitch and with distinct harmonics which are lacking in all the other notes.

There is a good deal of individual variation in song within this general pattern. Though Part 1 may consist of just one rather than two notes, it is apparently never omitted altogether. Part 2 is very variable but is apparently never omitted. Part 3 may be omitted altogether. Each individual, however, has a fixed song which is variable only to the extent that, when the motivation for singing is low, some elements, especially the terminal *weet*, may be dropped out.

The most striking thing about the different song-types is that birds with neighboring perches tend to have similar songs. Thus within a singing assembly there are typically a number of groups of birds each of which has a song-type recognizably different from the songs of the other groups. Figure 3 is a sketch map of the singing assembly where I made most of my detailed observa-

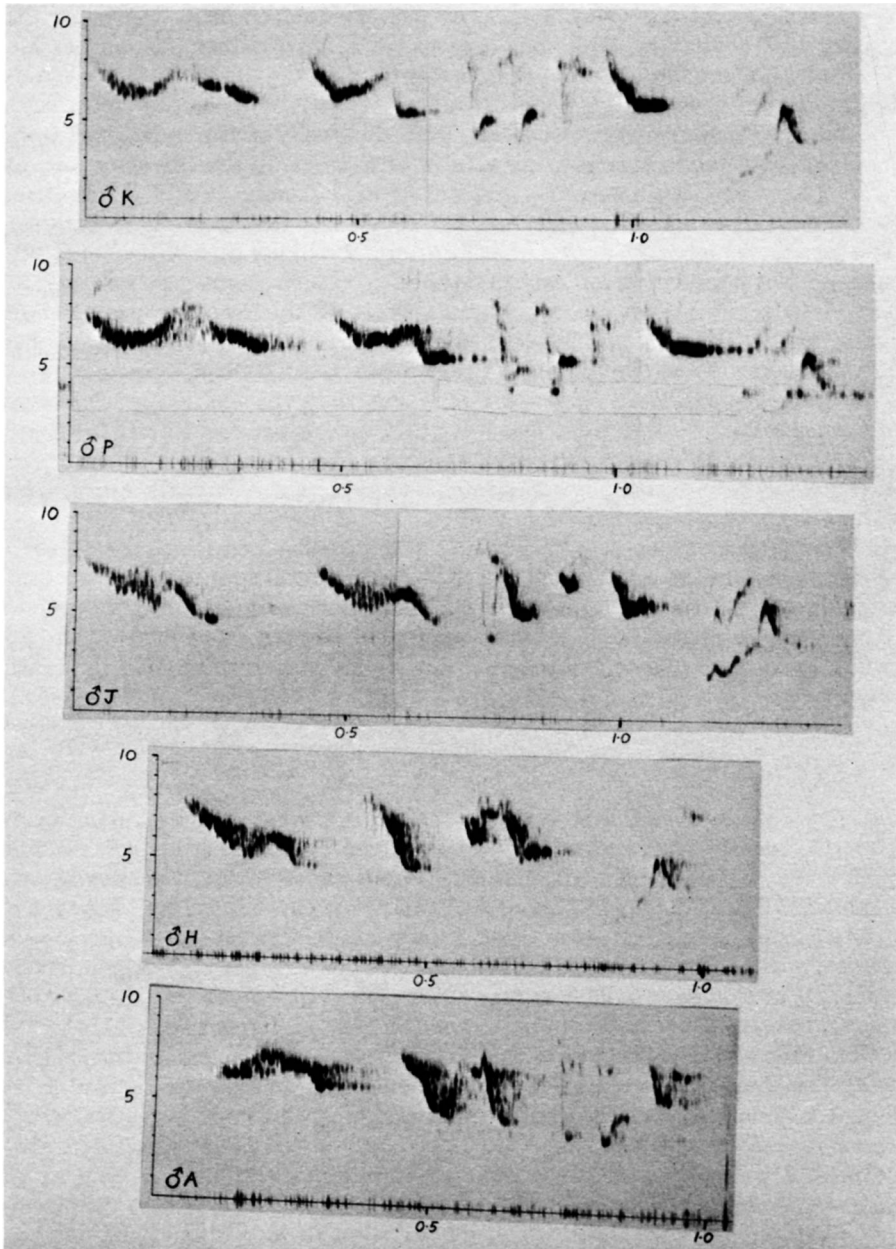


Figure 1. Spectrograms of the songs of five Little Hermits from the singing ground mapped in Figure 3. Vertical scale—kilocycles per second; horizontal scale, seconds. Note that Males K and P closely resemble each other as do Males G, H, and I. Male J, possibly a young bird, is different from both groups, yet most like Males G, H, and I.

tions, and Figure 1 shows spectrograms of the songs of five birds from this assembly. The very close resemblance between the songs of Males K and P, from the same group, is apparent. Male J, possibly a young bird recently settled, occupied a position between this group and the group of Males G, H, and I. It seems that the form of the notes in both the first and second parts of the song of Male J approximates that of the latter group. Figure 2 illustrates

the songs of four individuals in another singing assembly, and again the extraordinary similarity of the songs of Males a and b, which had neighboring perches, contrasts with the songs of two Males, c and d, from other parts of the singing ground.

Figure 3 demonstrates that birds with similar songs had perches mainly from 20 to 30 feet apart. Some outlying members of the groups were as close to members of different song groups as they were to members of their own, but to a large extent the song groups followed the spatial groupings of the song perches, which probably depended on the distribution of suitable perches and cover. This figure shows the distribution of song-types as they were early in 1960 when the singing assembly was in full activity. This distribution persisted virtually unchanged until July 1961, the end of the singing season. When I revisited the singing grounds in January 1963, three years after the map was made, nearly all the song-types which I was able to check were the same. I recorded some minor alterations however. On a new song perch, first occupied in November 1960, the occupant, Male L, in the beginning sang a song similar to that of Males K, O, etc.; later, in February 1961, the song at this perch was the same type as that of Males G, H, and I. Was there a different bird on Perch L? The songs at Perches E, F, and some of the outlying positions were less stable than the rest, and these perches were perhaps occupied by a succession of different birds. Song Perch Q was first occupied in June 1961 and the song at that time was rather simple; but in January 1963 the bird at this perch was singing a song identical to that of Males K, O, etc. Almost certainly the bird I recorded in June 1961 was a young one establishing itself.

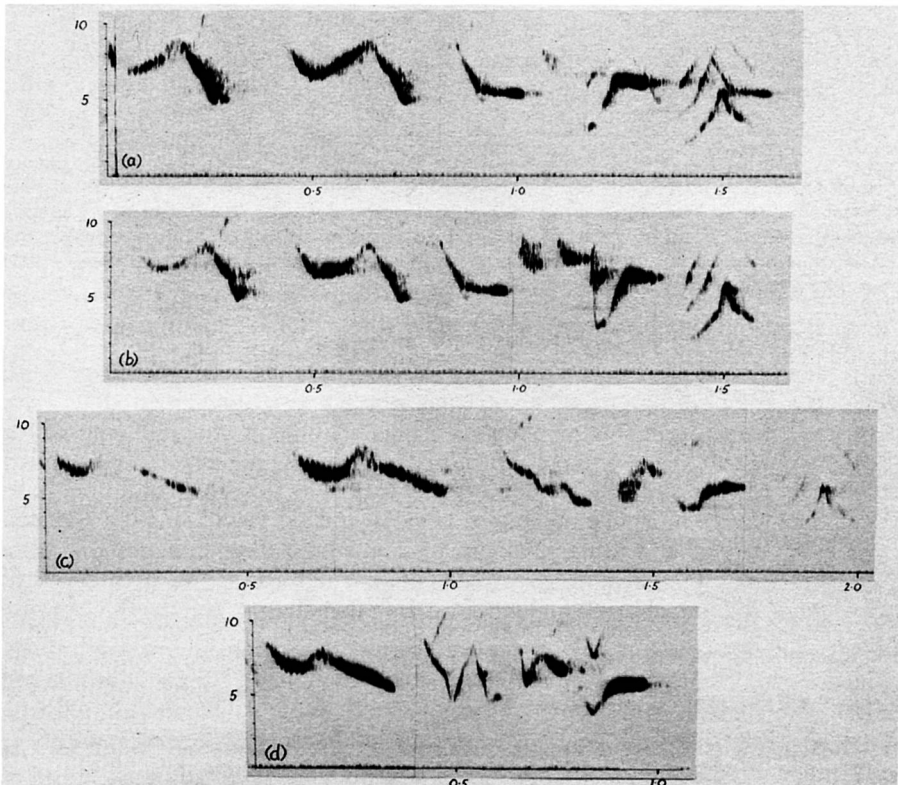


Figure 2. Spectrograms of the songs of four Little Hermits from a singing ground about three miles from that shown in Figure 3. Birds a and b occupied neighboring song perches; birds c and d were from other parts of the singing ground.

The persistence of the singing behavior of the individual birds was strikingly illustrated by Male K (Figure 1). He sang a song typical of his group, but tended to omit the terminal *weet* much more often than the other birds in that group, more and more frequently towards the end of a song-bout and also more and more frequently as the day wore on. A large number of counts throughout the day on 18 February 1960 showed that the incidence of the terminal *weet* declined fairly steadily from 80 per cent between 0600 and 0700 to 22 per cent between 1600 and 1700, while only 4 per cent of the few songs heard after 1700 included it. Three years later, in January 1963, the same song-type was being sung from this same perch. In contrast to the other birds in the group, which were singing full songs, the terminal *weet* was being omitted with about the same frequency as it had been three years before: in a bout of song at 0715, 87 per cent of the songs included the terminal *weet*.

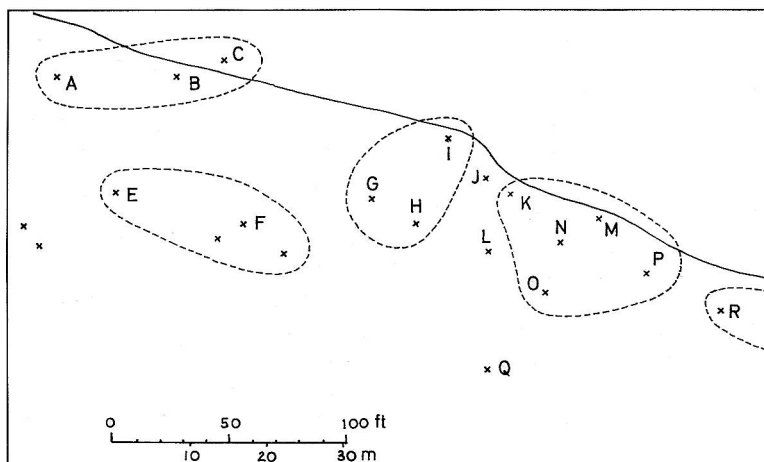


Figure 3. Distribution of song perches of Little Hermits in the central part of the singing ground where the recordings in Figure 1 were made, showing groups of birds singing recognizably different songs. The diagonal line indicates the crest of a steep-sided ridge with the song perches distributed mostly a little way down the south-facing slope. Letters mark song perches permanently occupied during the period of study. There were 28 in all. Crosses without letters indicate perches not consistently occupied.

From these and similar observations, there can hardly be any doubt that individual Little Hermits, when they acquire perches at a singing ground, develop a song similar to those of their nearest neighbors, and that, once acquired, this song persists unchanged. The distribution of suitable cover for song perches and the relatively long life of the adults are probably sufficient to account for the stability of the song groups at the singing ground over the years. The situation is to some extent parallel to that found in the Chaffinch (*Fringilla coelebs*) and other passerine species which have local song dialects (Thorpe, 1958), but on a much smaller scale, the dialects being confined to areas measured in hundreds of square yards rather than in hundreds of square miles.

Other Displays

Periodically, Little Hermits perform aerial displays above or in the vicinity of their song perches. These do not last very long, and some parts of them, being exceedingly rapid, are difficult to observe accurately. Since the sexes are for practical purposes indistinguishable and the birds were not

individually marked, I cannot elucidate the significance of the displays. Thus, I confine the following account to a brief description of the main movements supplemented by the observations of Skutch (1951) and Arp (1957).

The displays occur most frequently at the end of a singing bout. Characteristically, as the bird nears the end of a song-bout, it utters a few rather squeaky, hurried songs; then it may stretch on its perch and gape upwards. Finally, it rises from its perch, hovers, and may either fly straight off, presumably to feed, may move away slowly with its body upright, examining the undergrowth as it goes, or it may execute some striking aerial displays before departing. In the most usual display it holds the body horizontally with the neck stretched upwards, the tail pointing up, and the feet usually hanging down. The breast feathers may be fluffed out. In this boat-like posture the bird may move slowly for a few inches, then turn rapidly and move back the other way, and so on. This is often followed by one or more very rapid flicks downward towards the perch, each flick being accompanied by a soft *tock* after which the bird usually flies off. Whether the *tock* is vocal or mechanical, I cannot say.

In encounters which seem to be primarily aggressive, especially between males establishing themselves at a singing ground, chasing is frequent. Singing is intense, and a note very like the terminal *weet* may be uttered in flight. A perched bird, if approached aggressively by another, usually responds by intensifying its tail-wagging movements, fanning its tail, and gaping. Arp (1957) describes a low trilling uttered by both birds in such encounters, but I did not record this. Arp's account suggests that he was observing a singing assembly which was in a comparatively unsettled state, since his birds, when they stopped singing, regularly flew towards another bird, apparently aggressively. This was not usual in the singing assemblies where I made most of my observations. The boat-like flight and "tocking" do not seem to occur in aggressive encounters.

In encounters that appear to be primarily sexual, the display usually begins with one bird hovering in boat-like flight just over the other, which is perched. (I make no attempt here to say which bird is male or which bird is the "owner" of the perch.) The hovering bird may then make very rapid downward flicks, with a *tock* accompanying each flick, over the perched bird. Alternately, the two birds may change places in rapid succession. Or the perched bird may fly up and both birds move upwards, first one and then the other making little upward darts, as though they were attached by invisible threads. Skutch (1951) and Arp (1957) both describe variants of these maneuvers, the usual outcome of which is that, after some very confusing and rapid movements, both birds fly off.

Several times I observed birds, at the end of a song-bout, fly a little way from the perch and execute the downward flick, with *tock*, over a dead leaf. Arp also recorded this and mentioned that the leaf, or a piece of moss, was always the same one for each individual bird and tended to move in the slightest breeze. He also mentioned that a passing butterfly or a falling leaf might stimulate the display, suggesting that these observations not only show the importance of movement in stimulating display, but also help to explain the constant wagging of the white-tipped tail.

Skutch described two display sequences, apparently sexual, which took place away from a singing assembly. In one of these, in addition to the usual boat-like hovering posture with slow flights back and forth, the upper bird occasionally shot rapidly back and forth over a distance of a foot or two above the perched bird, making a loud buzzing noise with the wings.

We need many more observations and field experiments before the significance of these activities is clear, but I offer the following preliminary suggestions and hypotheses. Although no one has recorded copulation in the Little Hermit, it probably takes place on the display perch. This would be in agreement with what occurs in other "lek birds." Indeed, the singing assembly would be largely inexplicable if this were not the case.

The male must, therefore, first attract the female to his perch. Song achieves this, aided by the tail movements and perhaps, when the female is at close quarters, also by the gape. As Arp (1957) noted, the tail movements are intensified when another bird approaches a perched bird; and, in the undergrowth, the yellow gape may be more conspicuous than any part of the plumage. The female presumably approaches and hovers above the male. The male must then induce her to alight. This is probably the functional significance of the rapid change of place, which is sometimes seen between two birds at a perch, and is now sufficiently ritualized to occur at other times also—perhaps between two birds of the same sex.

The downward flick and *tock* of a hovering bird towards a perched bird is probably a precopulatory movement. When directed at a dead leaf or similar object, it may be redirected activity. The fact that such substitute objects are liable to shake in the breeze suggests that rapid tail-wagging by the female may be an important element in her soliciting behavior.

Finally, it seems significant that in each song-bout there is a gradual change from uninterrupted singing to more intermittent singing, accompanied by an increasing tendency to aerial displays as the bout draws to an end. It would seem that aggressive motivation is uppermost at the beginning and sexual motivation uppermost at the end of the bout.

There is ample scope for further field work on this species, which could lead to a more complete understanding of its complex social organization. Individual marking of birds, high-speed photography, and experiments using models will all be essential to such an investigation, as well as a more complete analysis of the song and other calls than is possible at this stage.

Summary

Singing assemblies of males are known in several species of hummingbirds of the genus *Phaethornis*, among them the Little Hermit (*P. longuemareus*). In the Northern Range of Trinidad, where this species is common, the assemblies are typically situated high up on the forested ridges. The singing grounds are traditional and within them the same song perches are occupied year after year.

The singing assemblies are active from November or early December to July when the post-breeding molt occurs. Throughout the active period, each male is at its perch for a high proportion of the daylight hours. One bird, for example, was present for 70 per cent of the entire time. While the bird is on its perch, it sings on the average of once every two seconds, or a total of about 12,000 songs per day.

The song, a high-pitched phrase lasting about one second, varies a good deal. Birds with neighboring perches tend to have similar song-types, and at one singing ground the distribution of the song-types persisted largely unchanged over a period of three years. This suggests that males, when they first acquire a song perch, develop a song similar to that of their nearest neighbors.

Several aerial displays are described and provisional suggestions made as to their probable significance. Much more detailed observation, and also

experimentation, will be necessary to clarify the relationships between the sexes and between the individual males at the singing assemblies.

Acknowledgments

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