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## BEHAVIORAL RESPONSES OF LONG-TAILED HERMITS (*PHAETHORNIS SUPERCILIOSUS*) TO SIMULATED TERRITORY INTRUSIONS

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**Abstract.** We studied the behavioral changes of Long-Tailed Hermits (*Phaethornis superciliosus*) in response to playbacks of songs of different rates. Different call rates seem to reflect different dominance statuses – males with higher call rates are more dominant. Dominant males apparently represent a greater threat to a territory holder, evoking a quicker defensive response. The resident song rate declined with time after intrusion, suggesting a leveling off to a steady state. However, there was no significant difference between the song rate of the resident male before and after intrusion. These behavioral responses provide some insight to the complex intralek interactions of Long-Tailed Hermits.

### INTRODUCTION (JAR)

In lek mating systems, several males establish and defend individual territories in close proximity to each other. Females visit these leks to mate, typically selecting the dominant males in the lek. This leads to competition between males for dominance, since dominance is associated with greater access to mates.

*Phaethornis superciliosus* is a lekking species in which the males sing repetitive one note songs from their individual territories to attract potential mates. Since there is little physical variation between males, the question arises as to what indicates male dominance in *P. superciliosus* leks. Previous studies have suggested that higher song rates may be indicative of male dominance (Stiles 1979).

We questioned what effects playbacks of songs of different rates in a male's territory would have upon the resident. Since males defend their territories from intrusions by other males, we expected that such playbacks would be perceived as an intrusion by a challenging male and evoke an aggressive response from the resident male.

Assuming that higher call rates are indicative of more dominant individuals, we hypothesized that perceived intrusions by dominant birds (fast song rate playbacks) would provoke a faster response than perceived intrusions by sub-dominant birds (slow song rate playbacks). This hypothesis was based on the assumption

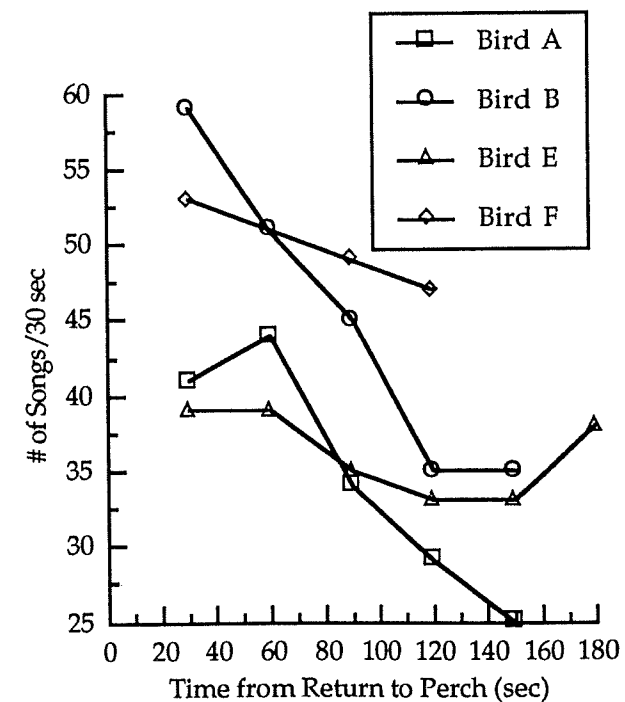


Figure 1. Scatterplot of song rate vs. time from return to perch for the fast song rate treatment.

that intrusions by dominant birds represent a greater threat to the resident individual. We also predicted that fast song rate playbacks would provoke longer duration of aggressive behavior than slow song rate playbacks.

Stiles (1979) found that as a result of an intrusion by another bird, the resident would respond by singing at a higher rate than before the intrusion. We expected, therefore, that birds would sing at a higher rate after the playback than before, and that the fast song rate playback would provoke a higher song rate than the slow song rate playback. We also expected to note a decline in the resident's song rate as it became less agitated with increased time after either treatment.

Finally, we hypothesized that call rates of resident birds would be negatively correlated with response time, since dominant birds should respond more quickly to intrusions than sub-dominant birds.

#### METHODS (EWG)

We conducted our experiments on a Long-Tailed Hermit lek on 8-9 February 1992 at Finca La Selva, Costa Rica. The lek was located approximately 300m from the biological station on the Sura Trail, in secondary forest with a moderate amount of undergrowth and a canopy ~20m high.

Before the study began, we recorded the songs of two different birds at a lek ~1km from the biological station on the CES trail. Both recordings were made ~4m from the bird with a condenser microphone on a Sony® WM-DGC using Dolby® C.

Six birds were studied individually in their territories during two

study periods on the first day. Only 4 of the 6 birds were studied on the second day because of a decrease in lek activity. The study periods corresponded to times of high lek activity: 0700-1000 and 1430-1630 (Stiles 1979). Preliminary observations lasted 4min, while standing 4-6m from a bird. The number of calls were recorded while the bird was perched. Time spent off the perch was also recorded as one measure of aggressive behavior. Observations stopped (and were continued later) when the male was not seen for 2min off his perch. Observations were discontinued at such time because it seemed unlikely that the resident could defend his territory when gone for long periods, such as when feeding.

Immediately following the observation period, one of two treatments were applied, in which recordings of either (i) a slow song rate (72 calls/min) or (ii) a fast song rate (118 call/min) was played. Treatments

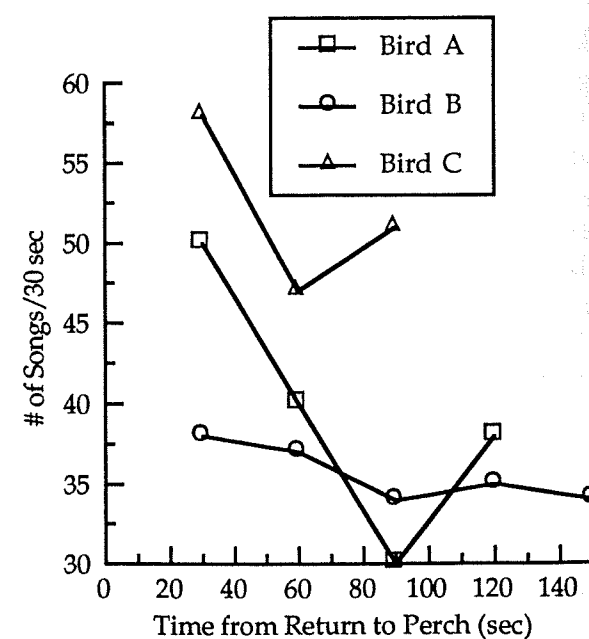


Figure 2. Scatterplot of song rate vs. time from return to perch for slow song rate treatment.

Table 1. Comparison of examined behaviors in slow and fast song-rate treatments.

Behavior		Fast treatment			Slow treatment		
		mean	s.d.	n	mean	s.d.	n
Time spent off perch (sec/min)	Before	10.25	10.6	12	3.8	6.7	12
	During	48.7	11.7	12	37.2	16.7	12
Response time (sec)	Entire day	11.3	11.7	12	22.8	16.7	12
	Morning	6.0	6.9	12	20.0	5.0	12
	Afternoon	16.7	14.4	12	25.7	25.4	12
Duration of defense behav. (sec)		89.8	34.4	5	68.0	59.1	3
Song rate after treatment (songs/60 sec)		96.8	16.7	5	97.3	20.1	3
Song rate before treatment (songs/60 sec)		88.6	19.8	5	84.7	6.1	3

were alternated during each study period, and no bird received the same treatment twice in one day. Dolby® C was used during playback on 2 Uni-Tone portable speakers at the same location as the preliminary observations. Volume was adjusted by ear to a constant level between treatments and the speakers were held at 1.25m height, a known perch height of the hermits (Stiles 1979).

Playback for each treatment lasted 1min, during which time the same data as in the preliminary observations were collected. Following playback, data collection continued for 4min, except that the number of calls was recorded at 30sec intervals. Distance between successive birds studied was maximized to avoid habituation to the playback of non-subject individuals within hearing range.

A map was constructed of the lek area, marking the positions of the study birds and others heard in the area. The number of calls in one minute was counted for the other birds during the afternoon of the second day.

#### RESULTS (JAR)

On the second day of the study, we observed that the study individuals

were not responding to the playbacks. Apparently, habituation to the playbacks was resulting in a lack of response. Since data taken on the second day could misrepresent *P. superciliosus*' response to intrusions, we did not use data from the second day in any of the following analyses.

To determine if *P. superciliosus* was responding to the playbacks, ratios of time spent defending the territory to total time were compared for before and during each treatment. We found a significant response for both treatments (fast:  $t=7.369$ ,  $p<0.001$ ; slow:  $t=5.587$ ,  $p<0.001$ ; Table 1).

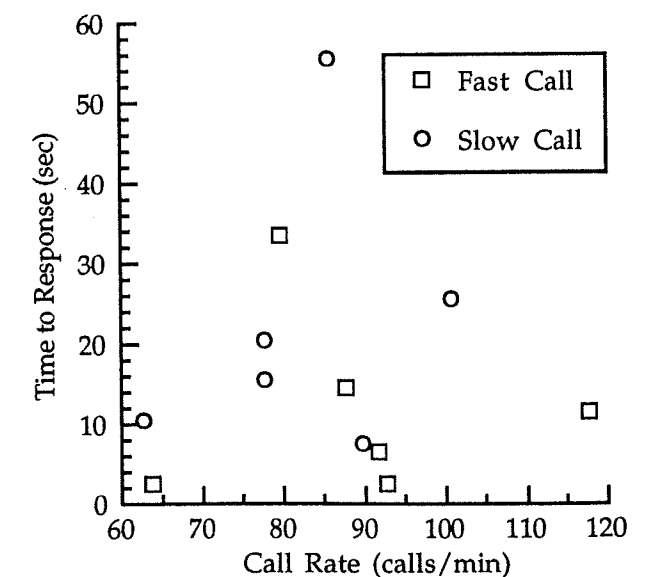


Figure 3. Scatterplot of response time vs. call rate for both fast and slow song rate treatments.

Response time was not significantly different between the two treatments ( $t=1.397$ ,  $p>0.2$ ; Table 1). However, since we qualitatively noticed that response time between the two treatments had been different in the morning, we then analyzed the morning and the afternoon separately. In the morning, response time to the fast song rate was significantly quicker than to the slow song rate ( $t=9.08$ ,  $p<0.001$ ). No significant difference was found for the afternoon ( $t=.534$ ,  $p>0.5$ ; Table 1).

The duration of defense behavior was not significantly different between the two treatments ( $t=.654$ ,  $p>0.5$ ; Table 1).

The song rates when the birds returned to their perches after the playbacks were not significantly different from their song rates before the

playbacks in either treatment (fast:  $t=.780$ ,  $p>0.4$ ; slow:  $t=1.039$ ,  $p>0.2$ ; Table 1). No significant difference existed between treatment type and song rate after treatment either (Table 1;  $t=.0026$ ,  $p>0.9$ ). We did find, however, a significant negative correlation between song rate and time from playback for the fast song rate treatment ( $r=-0.63$ ,  $p<0.01$ ; Figure 1) and a marginally significant negative correlation for the slow song rate treatment ( $r=-0.57$ ,  $p<0.6$ ; Figure 2).

We did not find significant correlations between the resident bird's initial call rate and its response time for either treatment (fast:  $r=0.34$ ,  $p>0.5$ ; slow:  $r=-0.03$ ,  $p>0.9$ ; Figure 3).

A map of individual birds' positions and their call rates (if known) did not suggest any obvious spatial patterning in regard to call rate (Figure 4).

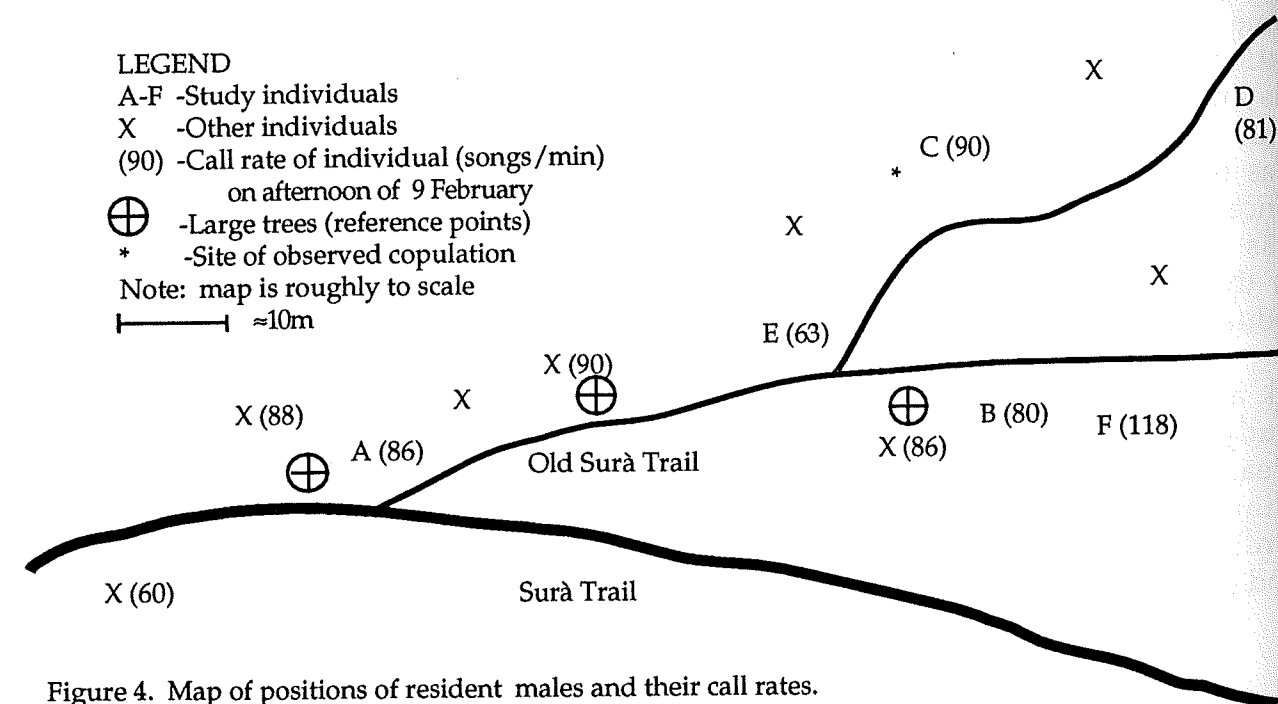


Figure 4. Map of positions of resident males and their call rates.

## DISCUSSION (JAR)

Since response time was significantly different between the two treatments in the morning, but not in the afternoon, or over the entire day, we believe that habituation to the playback was already beginning to occur during the afternoon of the first day. The difference in response time in the morning, however, does indicate that long-tailed hermits respond more quickly to an intrusion by a dominant male than a sub-dominant male.

The lack of a significant difference in the duration of the defense behavior between the two treatments suggests that once a defensive response is evoked from a territory holder, the amount of time that he spends defending the territory is not dependent upon the dominance status of the intruder, contrary to our initial hypothesis.

The lack of a significant difference between call rates before and after treatment and the significant (or nearly significant) negative correlations in song rate with increased time from treatment are contradictory findings. They suggest that males do not respond to intrusions by increasing their song rates, as hypothesized, but that their song rates decline with increasing time from the intrusion. This indicates that the song rates a few minutes after the treatment are below the song rates prior to the treatment. We have no explanation for this finding and it certainly deserves further study.

The lack of any correlation between the initial call rates of individu-

als and their response times has two possible explanations. The obvious possibility is that dominant birds simply do not respond faster to intrusions. The other possible explanation is that initial call rate is not indicative of dominance. We believe that the second explanation is more likely due to our observation of more frequent dueling between neighbors at high song rates, than between sub-dominant males. The conclusion also provides some insight into the complex interlek interactions in Long-Tailed Hermits. The finding may or may not be applicable to other species with lek mating systems.

Additional studies are needed to sort out the relationships between territorial intrusions and the behavioral responses of the residents. Future studies should look at more than one lek and, to avoid habituation, temporally space all playback treatments.

## LITERATURE CITED

- Stiles, Gary F. and Larry L. Wolf. 1979. Ecology and evolution of lek mating behavior in the Long-Tailed Hermit Hummingbird. *Ornithological Monographs* 27: 1-78.

## APPENDIX A (EWG)

We observed on 8 February 1992 a possible hermit copulation, which is noteworthy because of its rarity (Stiles and Wolf 1979). The female was perched and fluttered her tail through an approximately 90° angle across the horizontal plane. The male hovered 5-10cm in front of the female with his



body in a nearby vertical position. He fluttered his tail from front to back covering approximately a 30° angle that was a little to the right of vertical. Both wiggled their tails and bodies slightly from side to side. After approximately 15sec of this behavior, the male flew behind the female and mounted for less than one second. He flew in front of the female and the courtship behavior began again. After about 10sec he flew behind the female again and mounted for less than one second. They flew away in the same

direction. No vocalizations were heard during any of this behavior.

It seems likely that the male was bird C because the female was perched in his territory. Furthermore, he was present on his usual perch immediately before and after the copulation, but not during this time.

The female was perched on a horizontal branch about 1m high. It was fairly well covered by foliage from a liana and a bush. The mating took place at 0830 in overcast weather with a slight mist in the air.