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EFFECTS OF A MODEL ON LONG-TAILED HERMIT LEKKING BEHAVIOR

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Abstract

I studied the behavioral effects of the presentation of a model to male long-tailed hermits Phaethornis supercilious. I predicted that song rate would increase in the presence of the model. I did not obtain a significant difference between song rates in the presence and absence of a model. However, based on other observations I concluded that the model did affect the hermits' behavior. I believe this effect was not statistically significant because the birds' baseline activity level was already above the average level. I also found that the ratio of number of visual displays per minute to number of songs per minute decreased as the day progressed.

Introduction

Phaethornis superciliosus breed in a lek mating system (Stiles, 1979). These leks consist of a group of males; each defends a small territory containing singing perches. A prerequisite for lek evolution may be the fact that male long-tailed hermits take no part in the care of young (Janzen, 1983). Therefore, the males invest more energy competing for opportunities to copulate with females, who periodically enter leks in order to breed. Lek activity occurs daily in 3 sessions - dawn, late morning, and late afternoon. The session at dawn is the most important; males use this time to redefine their territories (Stiles, 1979). The other two sessions decline in overall activity, correlated with decline in nectar supply from flowers on which the long-tailed hermits feed (Janzen, 1983).

Hermit males seem to know the locations of other males' perches. They will sometimes challenge another male via singing, chasing, and visual displays, in an attempt to obtain a larger territory and therefore more breeding opportunities. It has been documented that when a resident male is challenged, his song rate increases from 60-70 songs per minute to 90-110 songs per minute (Stiles, 1979). If song rate does vary with the presence of an intruder, I hypothesized that the introduction of a model long-tailed hermit and a tape recording of its song would increase the song rate of the resident male. I also expected to see an increase in the number of visual displays performed by the resident male. My reasoning was that the resident male would feel threatened by the 'intruder' and defend his territory. However, there was also the possibility that the male would consider the model to be a female willing to copulate and would attempt to mount it.

Methods

I studied the lek of long-tailed hermits at the junction of the Sendero Sura and the trail to the laboratory at La Selva, Costa Rica on 9-11 February 1991. I collected data during the 3 active lekking periods: dawn (0615-0750), later morning (0845-1130), and afternoon (1530-1745). Equipment included a flashlight and a model hermit. The model was a dead hermit, and was frozen between each session. I also used a recording I made of hermits singing the short song that is sung repeatedly on the lek. Henceforth I will refer to the model and recording together as the 'model'.

Each session I chose a bird that was singing at the time I began my data collection. In the first session I collected baseline data on 4 different birds; in all other sessions I studied only one bird. I observed 4 different birds in a total of 6 sessions; one bird was used twice, at different times of the day, and in one session the model was not presented.

To begin trials, I sat on the trail and counted the number of songs sung by the focal bird per minute (song rate). I ran at least 10 of these 'baseline data' trials in each session. During these trials, I noted the location of each perch the focal bird used (Figure 1). Next, I attached the model hermit to a tree branch within 1 meter of one of these perches, chosen arbitrarily. I played the tape recorder as close as possible to the model (usually within 1 meter). I sat within 10 meters of the model and observed the focal bird. I noted other observations as well, particularly visual displays: floats, defined as a bird hovering back and forth in front of a perched bird, and perch exchanges, when 2 birds switched turns perching in quick succession until one flew away. Many times resident birds chased foreign birds out of the resident's territory; these were not considered displays (Stiles, et al., 1979). I recorded other specific incidents, as well; these are noted in results.

Results and Discussion

I compared song rates in the presence and absence of the model using Mann-Whitney U-tests. There was a significant difference between the two song rates during the late morning session on 10 February 1991; all other tests were not significant (Table 1). Initially, this result seems to indicate that the model did not have a great influence on the birds' singing rates, which fails to support my hypothesis. However, this result can be interpreted in a different way. The birds may not have sung more rapidly in the presence of the model because the average baseline rate for birds in this study was already 95.87, which is much higher than the 60-70 songs/minute previously documented. In fact, this rate lies within the range of 'high activity' rates of 90-110 songs/minute (Stiles, et. al., 1979). In addition, while collecting baseline data I observed many chases and visual displays between the birds, indicating a high activity level. If the hermits had not

perceived the model as a threat, their song rates may have decreased instead. Perhaps the hermits simply maintained the high song rate preestablished by the presence of other birds in the area.

Further evidence that the birds responded to the model was obtained from other observations I made during the course of the study. The most intense responses to the model that I observed were 2 instances when the focal bird pecked at the model. The most common response was floating; I observed 34 incidences over a total of 251 minutes of observation while the model was set up (0.13 floats/minute). This number is high, considering that each float usually lasts for at least a few seconds, and one lasted for 76 seconds. At these times the the focal birds were facing the model within close range (< 1 meter). Another behavior illustrating that focal birds noticed and responded to the model was less direct - desertion of perch. For instance, some birds spent a great proportion of time at a single perch. If I set up the model at that perch, the bird under observation flew to a different perch and spent a disproportionate amount of time at that perch. When I moved the model to this second perch, the bird either flew to a third perch or returned to the first. One bird did this 4 times. This desertion behavior is quite opposite of the typical direct responses to the model, and may be an interesting topic for further study.

Long-tailed hermits' activity levels decrease as the day progresses, coinciding with the decrease of nectar supply in the flowers from which they feed (Stiles, et al., 1979). To see if there was a similar trend in my data, I used a Mann-Whitney U test comparing baseline song rates in the early morning session versus the afternoon session, assuming that song rate was indicative of general activity level. I chose to compare these two sessions because they would have the greatest difference in song rate. I did not obtain a significant C value ($n = 20$, $n_2 = 11$, $C = 113$, Crit. $U = 151$, $p > 0.05$). This result can be explained by the small sample size. Individual trends are usually more difficult to detect than group trends (Stiles, et al., 1979).

Another documented trend in the daily lek cycle is the ratio between number of visual displays and song rate; this ratio decreases during the course of the day (Stiles, et. al., 1979). I calculated these ratios for each of the 3 different times of day and obtained a strong decreasing trend, supporting the theory (dawn = 0.40; late morning = 0.27; afternoon = 0.15). Based on my previously described comparisons between song rates at different sessions, indicating that song rate does not change significantly during the course of a day, I conclude that the declining ration between the number of visual displays and song rates is primarily due to a decrease in display rate. As the supply of flower nectar decreases during the day, the necessity for a bird to conserve energy increases. I presume that a visual display requires a greater energy investment for a bird than singing does. Therefore, as a bird's energy level declines, the most efficient way for the bird to conserve energy while continuing to defend its territory is to significantly decrease its display rate

while either maintaining or slightly decreasing its song rate.

A factor contributing to possible sources of error in my study was the time constraint. Instead of doing many replicates on a single bird, I studied as many different birds as possible so as to get a more representative sample of the long-tailed hermit population. However, I still had a relatively small sample size (n=4), which gives my inferences about the hermit population as a whole less validity. In addition, my ability to discern the birds and distinguish the various behaviors increased as the study progressed, so I may have mislabeled or overlooked some behaviors during the earlier sessions of my study.

Lek territories are a basis for individual reproductive success in the long-tailed hermit; a territory of greater size provides a greater chance that a female hermit will enter the male's territory to mate. Accordingly, it is necessary for hermit males to respond to foreign birds in their territory. The males appear to distribute their energy efficiently, performing territorial displays requiring more energy when energy level is high, and vice-versa. Since a male long-tailed hermit does not participate in the rearing of young, he can better afford to expend this energy competing for mates; it ensures that he will gain more benefit with less energy cost, resulting in greater individual reproductive success.

Table 1 Mann-Whitney U Test results, comparing song rates in the presence and absence of a model.

Date	Bird Studied	C	Critical U	Signif.
2/9/91	#1-P.M. (A,B,C,D)	--	---	(No model)
2/10/91	#2-Early A.M. (B)	24.5	29	---
2/10/91	#3-Late A.M. (C)	92.5	91	0.05
2/10/91	#4-P.M. (A)	51.0	59	---
2/11/91	#5-Early A.M. (D)	12.5	14	---
2/11/91	#6-Late A.M. (B)	72.5	77	---

Session #	n_1*	n_2*	Song Rates (in songs/min.) Pre-Model Presentation	Post-Model Presentation
1	20	---	---	---
2	6	6	110.17	107.33
3	7	18	90.14	94.00
4	19	4	97.58	90.25
5	5	3	85.80	75.00
6	7	15	97.42	99.20

*-n_1 and n_2 are the number of one-minute trials used to calculate song rates. Some trials were discounted because birds left perches mid-trail. n_1 is pre-model; n_2 is post-model. When using Mann-Whitney U tests, some of these values were rearranged so that n_1 was the greater of the two numbers.

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Figure 1 Map of site. Lettered areas indicate estimated territory for each bird.
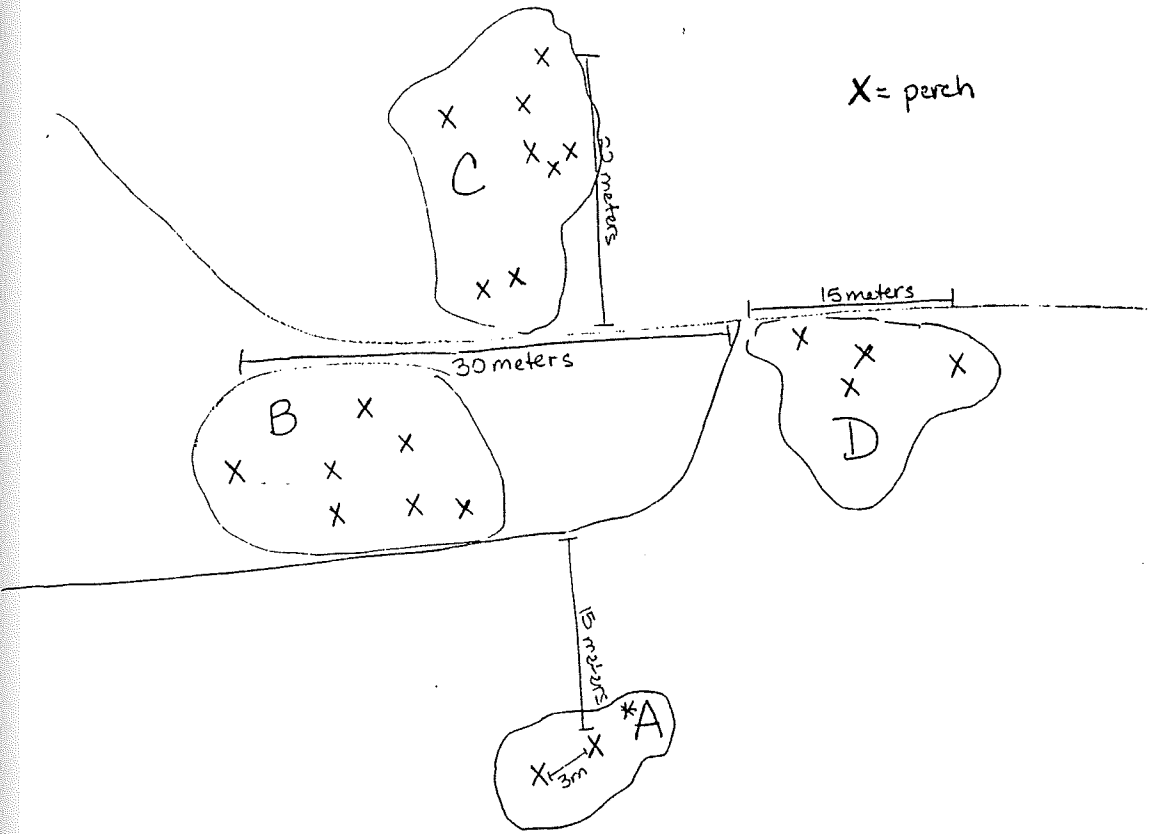
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