Discussion

Dung beetle abundance was greater in the early successional forest than in the primary forest, perhaps because of greater cover and food availability provided by the dense shrubs in this habitat. We observed that the 3 – 5 year successional forest had more dense herbaceous growth than primary forest. Dense shrubs may provide dung beetles with protection from predators and desiccation. In addition, dense shrubs may also provide cover for small mammals such as agoutis and other small rodents that produce food for beetles. Thus, dung beetle abundance may be greater in the early successional forest because dung may be more abundant there than in the primary forest.

The intermediate disturbance hypothesis (Connell 1978) suggests that an intermediate frequency of disturbance leads to increased species richness by allowing for the colonization of many species while preventing the exclusion of others by the dominant species. In accordance with this concept, we found the greatest dung beetle diversity in the secondary growth forest, where the frequency of disturbance falls between the two other forest types, and thus allows for the coexistence of many species of varying degrees of dominance.

In our experiment to test the effects of competition that may influence dung beetle distribution, proportional beetle mass changes were negligible and similar between the treatments. Thus, we could draw no conclusions comparing the relative levels of interspecific and intraspecific competitions. The competition experiment was initiated approximately 30 h after the first batch of individuals was collected. The confinement of beetles in plastic cups for this duration of time may have placed stress on the beetles that led to low levels of consumption. Some beetles, such as *Dichotomius* sp. that occurs commonly in the low elevations (Howden 1983) and was observed in our sampling, are nocturnal foragers. Thus, beginning our experiment at 03:00, after the majority of their foraging time had passed, may also explain why we observed negligible changes in body mass. Further study of competition could consider developing *in situ* methods for testing competition in order to minimize potential effects of experimentation on beetles. *In situ* studies would allow one to test how differing resource distribution across forest types may drive competition, and thus have important implications for beetle distribution.

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The effects of weather on the display activity of male white-collared manakins (*Manacus candei*)

Margaret L. Grace and Dominic Stanculescu

Abstract: Male white-collared manakins gather in leks, in which they perform wing-snapping displays to attract mates. Based on observations of others, we hypothesized that increases in light intensity would result in increased display activity. We examined the way in which activity rates of three leks in La Selva Biological Reserve changed with variation in precipitation and light levels. Rain had a significant negative effect on activity. In periods of great variation in light intensity, changes in activity were not correlated with the changes in light level, and even during periods of consistently low light, activity rate varied markedly. Further study is necessary to determine, however, if greater variations in light intensity on less overcast days effects display activity.

Key Words: calling behavior, lekking, mate-attraction, natural light intensity

Introduction

White-collared manakin (*Manacus candei*, Pipridae) males aggregate into assemblies to perform courtship calls, displays and wing-snaps to attract females to leks (Stiles and Skutch 1989). These display patterns occur in apparently sporadic bursts of activity (Hughes et al. 1991) with peaks between 09:00 - 09:30 and 14:00 - 14:30 (French et al. 1999). Previous studies have shown that the greatest density of leks in La Selva Biological Reserve, Costa Rica were found in secondary growth forests bordering abandoned pastures (French et al. 1999) and that display courts received a "fair amount of light through sunspots" (Wray et al. 1995). It has therefore been suggested that habitat light intensity may be a factor determining lek location (Wray et al. 1995). Studies on the white-throated manakin (*Corapipo gutturalis*) have indicated that sunspots may be preferred as display sites by males because they serve as spotlights on their performances to make them even more apparent to potential mates (Thery and Vehrencamp 1995). We hypothesized that diurnal variation in light intensity would affect the rate of manakin calls and wing-snaps. We predicted that high natural light intensities coming through the canopy would stimulate manakins to increase their calling and wing-snap rates to take advantage of the resulting increase in visibility to further attract females.

Methods

We located three manakin leks in La Selva Biological Reserve, Costa Rica, on the Sendero Oriental (SOR), the Sendero Atajo (SAT), and the Sendero Tres Ríos (STR), based on a map of known leks (French et al. 1999). At two of the leks (SAT 600 and SAT 940), we monitored the light intensity in sun-flecks on the forest floor using a light meter (Fluke 25 Multimeter), and recorded the number of audible wing-snaps and calls made by male manakins in the leks every 30 s during 45 continuous minutes on 15 February 2001. At the third lek (SOR 325) we recorded light intensity, wing-snaps and calls every 30 s for a total of 271 min on 16 February 2001. The cloud pattern was patchy in the early afternoon of 15 February, permitting several high-light recordings; the afternoon of 15 February, however, was overcast. In the morning of 16 February it rained continuously for 80 min, beginning 12 min after our sampling began. The later morning and afternoon were continuously overcast.

To simplify graphs of activity and light levels across time, we summed the number of

snaps and calls in 2-min intervals, and took the mean of the light intensities over the 2 min for each of the four study periods.

Results

Each sampling period was analyzed separately because we were unable to determine the number of males on each lek, and French et al. (1999) found that male manakin activity levels were positively correlated with the number of males present in a lek. Calling and wing-snapping activity varied greatly within all of our sampling periods despite the fact that light intensities were fairly constant in three out of the four sampling periods (Figs. 1-4). The examination of graphs of the 2-minute interval variations in calling, wing-snapping, and light over time, reveals several consecutive increases followed by decreases in activity, appearing as "bouts" of higher calling and snapping rates in all of the sampling periods. These bouts of higher activity rates do not, however, appear to be correlated with increases in light levels (Figs. 1-4). The absolute calling rates were not correlated with light levels across any of the sampling periods ($0.89 > P > 0.57$). The absolute snapping rates were not correlated with light levels in two of the four sampling periods ($P = 0.74$ and $P = 0.94$, Figs. 1 & 2), and were only correlated during the intermittently rainy morning and afternoon sampling periods of 16 February ($r^2 = 0.17$, df = 1, $P < 0.0001$, Fig. 3 and $r^2 = 0.12$, df = 1, $P = 0.034$, Fig. 4 respectively). Changes in light levels were not correlated with changes in the rate of calling ($0.71 > P > 0.51$) or snapping ($0.92 > P > 0.45$) in any of the overcast sampling periods, but in the sample in which sunbreaks occurred, change in snapping rate was positively correlated with change in light ($r^2 = 0.18$, df = 1, $P < 0.0001$). Possible delays in response to light levels are not visually apparent on the graphs, and comparisons of light levels during periods of high and low manakin activity (which may cover the delay in response) showed no difference for three

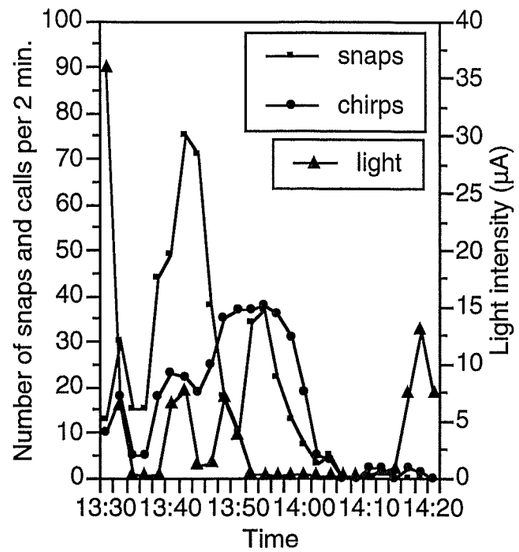

Fig. 1. Calling and snapping rates of the white-collared manakins in relation to light variation on a lek at 640 m on the Sendero Atajo, La Selva Biological Reserve, Costa Rica, on the sun-patched afternoon of 15 February 2001.

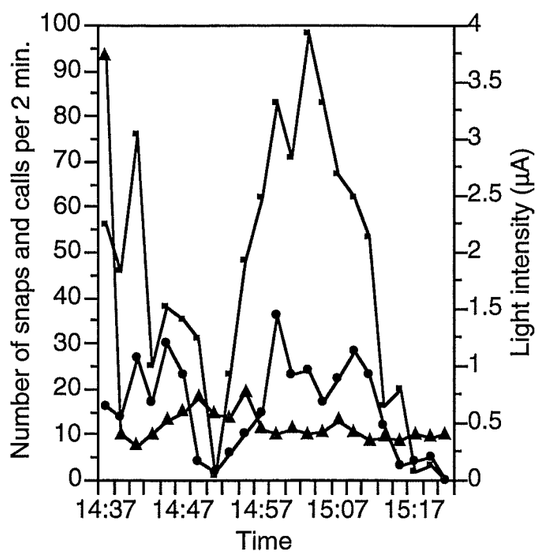

Fig. 2. Calling and snapping rates of the white-collared manakins in relation to light variation on a lek at 940 m on the Sendero Atajo, La Selva Biological Reserve, Costa Rica, on the overcast afternoon of 15 February 2001. Line symbols the same as for Fig. 1.

of the four sample periods ($0.66 > P > 0.07$). The significant difference between light levels occurred only when rain concurred with low light levels on the morning of 16 February (ANOVA, $F = 46.44$, df = 1,376, $P < 0.0001$, Fig. 3).

Manakin activity level was significantly lower during periods of rain (Welch's ANOVA, $F = 23.02$, df = 1, $P < 0.0001$, Fig. 3a-b). Snapping rate and calling rates were positively correlated only during the one sampling period when clouds were patchy and high-light periods were recorded ($r^2 = 0.24$, df = 1,101, $P < 0.001$; for all others $P > 0.05$, Fig. 1). The variation in the ratio of snaps to calls

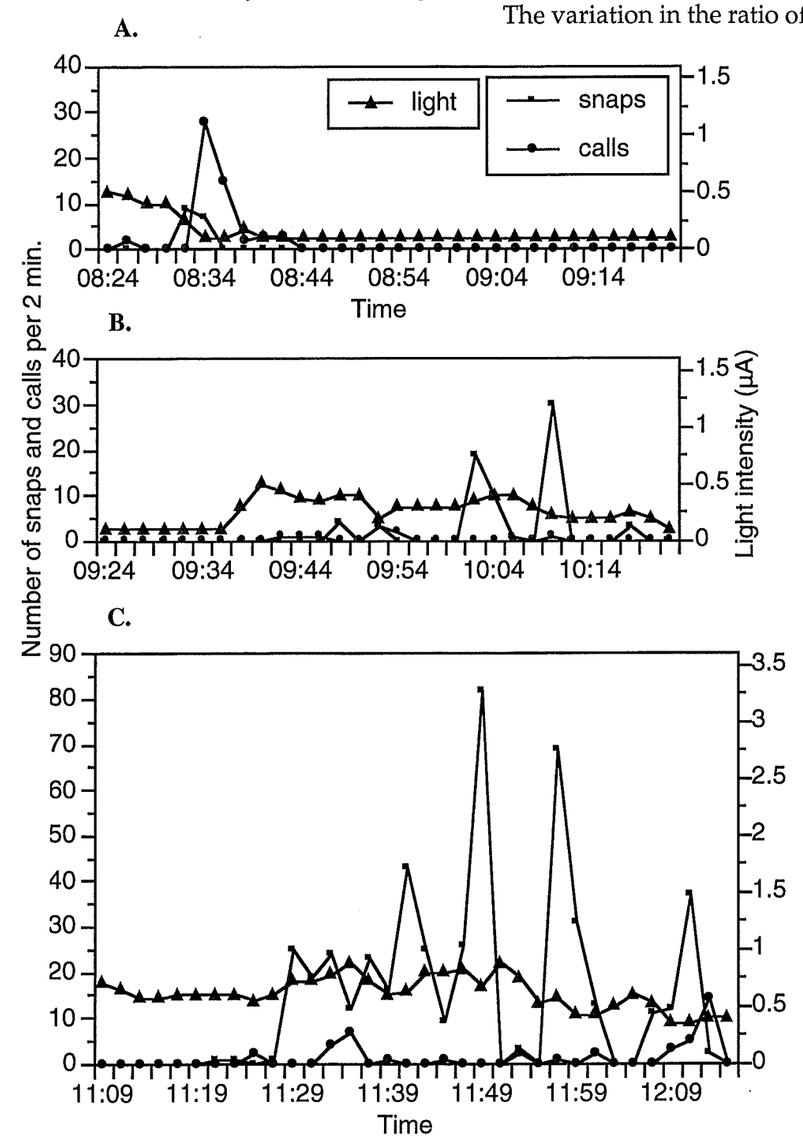

Fig. 3. Variation of light, and calling and snapping rates of the white-collared manakins in a lek at 325 m on the Sendero Oriental, La Selva Biological Reserve, Costa Rica, during three time intervals (A, B and C) on the rainy morning of 16 February 2001.

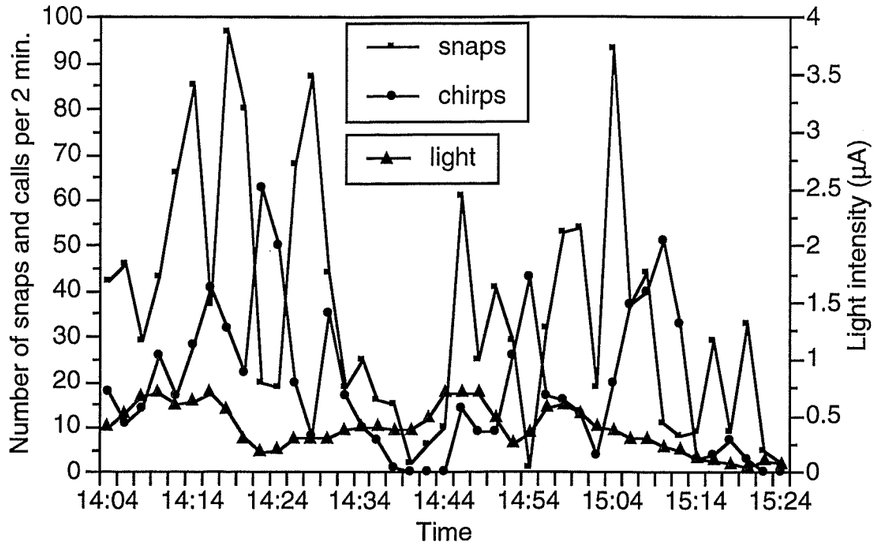

Fig. 4. Calling and snapping rates of the white-collared manakins in relation to light variation on a lek at 325 m on the Sendero Oriental, La Selva Biological Reserve, Costa Rica, on the overcast afternoon of 16 February 2001.

across time and between sampling periods did not have a discernible pattern.

Discussion

White-collared manakins greatly decreased their level of display activity during periods of rain: not only was activity lower during rain in the SOR 325 lek (Fig. 3), but because of the persistent rain during our study we were unable to locate most of the regularly-occurring leks in the La Selva forest reported by French et al. (1999). The general cloudiness during the period of the study may have resulted in an overall reduction in activity level of the manakins in the forest.

Increases in light levels during the studies, however, did not appear to cue the manakins to increase their displaying rates. This lack of demonstrated effect may be due to the conditions during sampling: the weather was rainy and overcast for all of the sampling periods except for one, in which the sun appeared for short periods of time. The variations in light levels during sampling, therefore, may not have been enough to cause an observable difference in manakin behavior. On the other hand, constant light levels did not mean constant activity levels in the leks monitored; periods of no measurable activity were sometimes followed by periods of intense activity without any change in light levels. Some other stimulus may therefore be cueing the birds to increase their rates of display irrespective of light intensity, e.g. the arrival of a female manakin. Sampling needs to be repeated during periods with greater light variation before it is possible to make the inference that light intensity has no effect on display behavior.

Further investigation of the way in which display rates change with time should take into account the different types of activity of the birds. We measured numbers of wing snaps and vocalizations without differentiating between types of snaps or vocalizations, but the different noises may serve purposes other than mate-attraction and may therefore be affected by stimuli other than those affecting the noises made during displaying. The demonstrated variation of display rate indicates that future studies of

manakin activity level should be careful to sample leks many times in a wide range of conditions when taking measurements of activity per lek in order to obtain an accurate picture of the activity level for each lek.

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