only what their bodies - particularly their antennae - touched, as they would frequently pass within several cm of the food displays without diverting their course. Perhaps the high proportion of ants returning to the nest with nectar was due to ants finding nectar sources in the canopy more frequently than they encountered insect prey.

I also observed that the proportion of ants carrying each food type was not consistent over short time periods within the 10 min natural foraging observations. I would frequently observe a "run" of several ants carrying insect parts to the nest, followed shortly by several ants carrying nectar. In the experimental food preference trial, I observed up to eight ants aggregating around a single food source, although they were not recruited by the foraging ant laying down a pheromone trail. It is possible that *P. clavata* searches for the first food type encountered and then alerts other colony members to the location of the food, so the food can be partitioned and transported to the nest.

I did not observe any aggressive behavior among ants within the aggregations around the food source. By using their antennae, newly arriving ants would communicate with ants around the food resource, and the feeding ant would move so that both could forage at the same time. When space did not permit all ants to forage simultaneously, the extra ants would wait for the other ants to finish eating before working their way to the food resource. This behavior is contrary to the aggressive interactions seen among many predatory and scavenging animals, and may be due to the eusocial nature of these ants.

That *P. clavata* attacked and killed the caterpillar prey indicates that it is not simply scavenging for dead insects, but is capable of killing them when encountered. The success rate of *P. clavata* encountering and killing prey was low (less than 50 %), perhaps due to poorly developed hunting senses such as vision.

The results of this study indicate that although certain food types may be more beneficial to *P. clavata* energetically, their sensory input is limited to whatever food items they encounter. *P. clavata* therefore forages on whatever is first encountered, regardless of the proximity of a potentially more beneficial food type.

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The distribution of white-collared manakin leks among different habitat types at La Selva

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Abstract: Male white-collared manakins, *Manacus candei*, aggregate in leks where they display to attract females. We predicted: (1) there would be a greater proportion of leks in secondary forests than in primary forests because understory characteristics such as the abundance of stems may provide more areas suitable for display; (2) more males would aggregate and display more in these preferred habitats; and (3) in leks with more males, the per male activity level would increase due to increased competition between males for potential mates. We located 11 leks and found that disproportionately more of them (73%) were located in second growth forests bordering abandoned pastures. Although the number of males and the activity per male did not differ between the more preferred habitat and other habitats surveyed, mean activity per male did increase with increased number of males. It seems that the vegetative composition of habitat may influence lek placement.

Keywords: *hotspot*, Manacus candei, *lek habitat associations*

INTRODUCTION

Males of some bird species aggregate in leks where they display to attract females. The white-collared manakin, *Manacus candei* (Pipridae), forms leks of up to 15 males, each with an individual court (Stiles and Skutch 1989; *pers obs*). The courts are elliptical patches of cleared ground up to 1.2 m long, in which males jump and fly between small saplings, brush, and small vines snapping their wings and calling to attract females (Stiles and Skutch 1989).

We predicted that white-collared manakin leks in La Selva would be non-randomly distributed, with a greater proportion in secondary forests than in primary forests because the denser understory may provide greater amounts of suitable display areas. Furthermore, we predicted that more males would aggregate in the more preferred habitat of secondary forest and lekking display activity would be higher there. Finally, we predicted that in leks with more displaying manakins, the per male activity level would increase due to competition between males for potential mates.

METHODS

On 15-18 February 1999, we surveyed the area within 50 m of each side of most trails at the Estacion Biologica La Selva (trails marked on Fig. 1), and located white-collared manakin leks. When a lek was found, we recorded its location relative to the 50 m distance trail markers, the number of male birds displaying at the lek, and the amount of displaying activity during a 5 min trial. Activity was defined as the total number of chirps and wing snaps made by all males in the lek. After locating a lek, we waited for 1 min to allow the manakins to acclimate to the observer. If the manakins did not resume displaying immediately, we waited until displaying resumed (usually within 15 min). At each lek, activity levels were quantified during three, independent 5 min trials, with at least 30 min between trials. Mean activity per male was then calculated by dividing the mean activity during the three, 5 min trials by the number of males in the lek.

Lek location was entered into the GIS system at La Selva by Matt Clark, GIS Manager, and overlaid with a map of the habitat types. The forest composition of our survey area (50 m on either side of all surveyed trails) was quantified from the GIS database for La Selva, and the percentage of each forest type calculated. Lek locations were then compared with these values using a Chi-Square test.

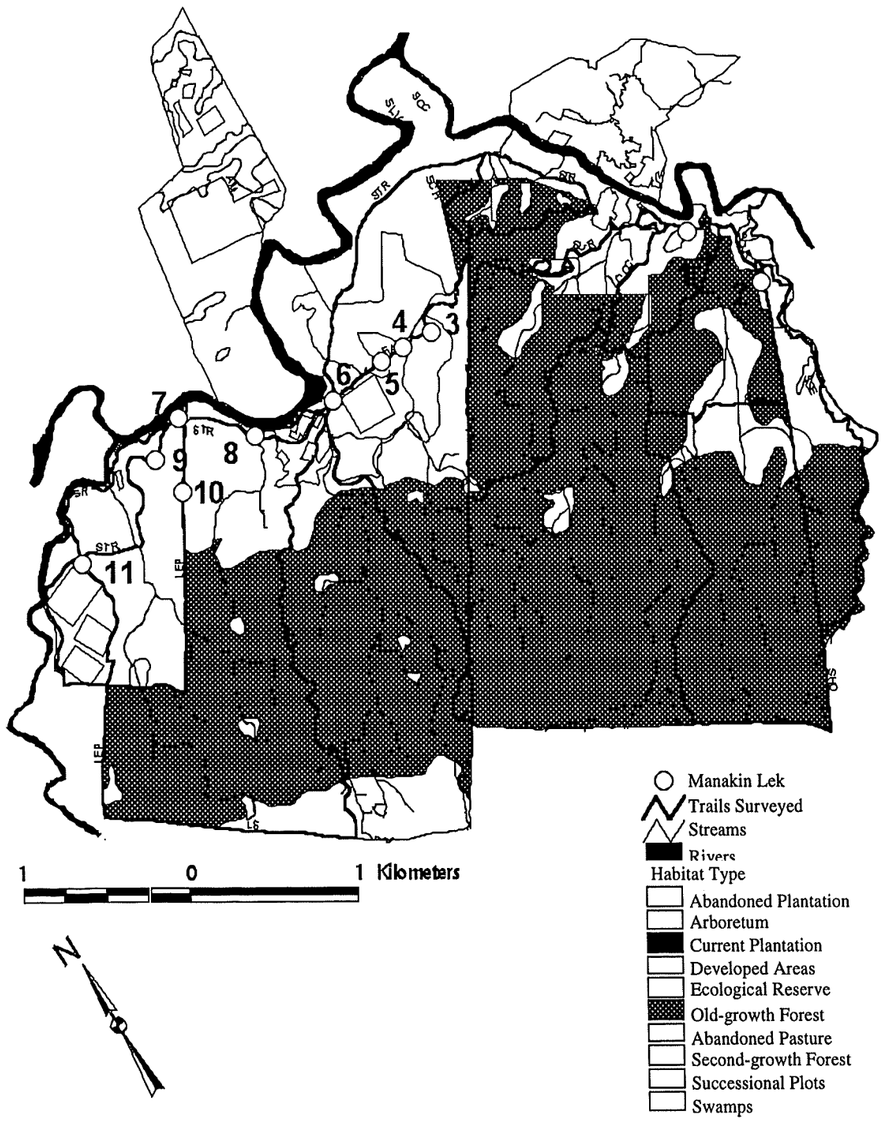

Fig 1. Map of La Selva habitats, White-collared manakin lek location, and trails surveyed at Estación Biológica La Selva, Costa Rica. Lek number, locations, and characteristics are listed in Appendix 1. Trails were surveyed 14-17 February 1999, 50 meters on either side of the trail.

RESULTS

All leks were located in four of the 10 habitat types surveyed (Table 1, Figs. 1 and 2). All four habitats could be considered under the broad classification of secondary growth habitats (Fig. 2). White-collared manakin lek distribution at La Selva was non-random, with 72.7% (8 of 11) of leks located in second growth forests bordering abandoned pastures (G-test: X^2=780.8, df=4, P<0.0001). If leks were distributed in habitats in proportion to their occurrence, only 17% of the leks would be expected in that habitat.

Contrary to our second hypothesis, the number of males and the mean activity per male did not differ between the more preferred habitat of second growth forests bordering abandoned pasture and males in other habitats (X^2=0.89, df=1, P=0.34 and X^2=0.64, df=1, P=0.43, respectively). However, mean activity per male did increase with increased number of males (r=0.64, df=1,8, P=0.045; Fig. 3).

Table 1. Location and basic characteristics of white-collared manakin leks at Estacion Biologica La Selva, Costa Rica. Mean activity was defined as the number of snaps and number of chirps heard in three 5 min trials. Maximum activity is the value from the observation period that had the most snaps and chirps.

Lek #	Trail Name	Location	Habitat Type	# Males	Mean Activity	Max Activity
1	Sendero Oriental	325-250	Second-growth	5	53.8± 25.6	129
2	Sendero Holdrige	140	Successional Plots	7	59.7 ± 18.7	97
3	Sendero el Atajo	600	Abandoned pasture	4	29.0 ± 4.2	35
4	Sendero el Atajo	800	Abandoned pasture	4	56.7 ± 38.1	132
5	Sendero el Atajo	900-1000	Abandoned pasture	7	97.3 ± 24.9	143
6	Sendero Tres Rios	2725-2775	Abandoned pasture	8	66.0 ± 22.9	101
7	Sendero Tres Rios	3850	Abandoned pasture	2	*	*
8	Sendero Tres Rios	3300-3400	Second-growth	6	119.7 ± 35.8	180
9	Sendero Tres Rios	4100-4200	Abandoned pasture	5	91.0 ± 19.1	127
10	Lindero el Peje	475-550	Abandoned pasture	11	113.0 ± 98.2	309
11	Sendero Tres Rios	5250	Abandoned pasture	3	37.3 ± 4.3	45

* Lek was observed only during pilot study.

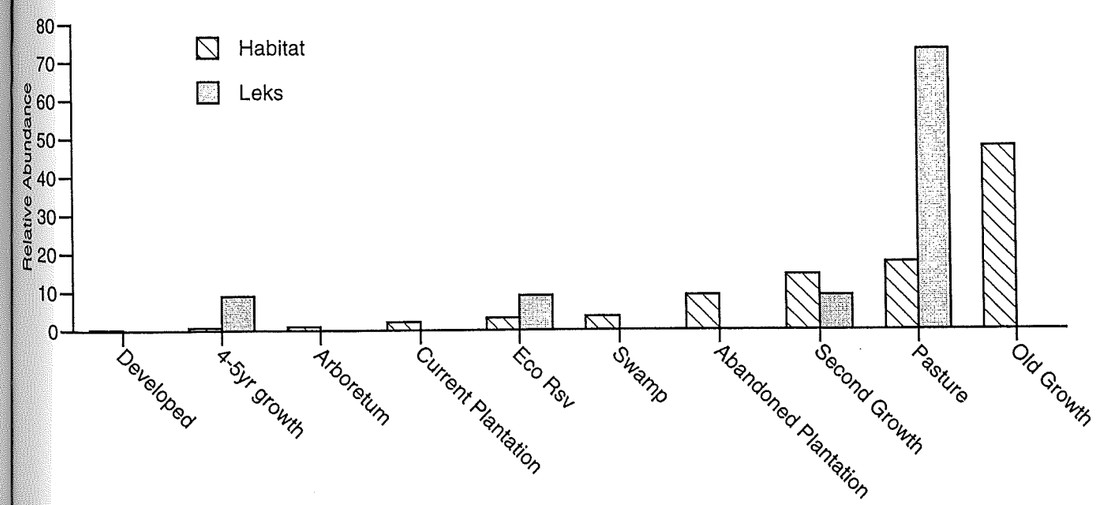

Fig. 2. Comparison between relative abundance of different habitat types and percent occurence of white collared manakin leks within those habitats at Estacion Biologica La Selva. The distribution of leks is not random (P < 0.0001).

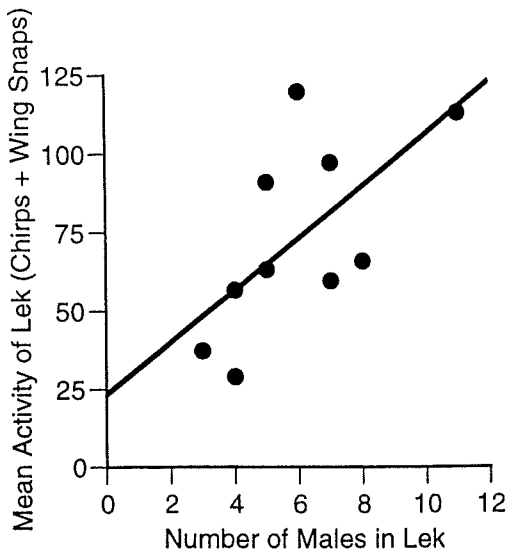

Fig. 3. Mean activity (Chirps + Wing Snaps in a 5 min period) in white-collared manakin leks at Estacion Biologica La Selva was positively correlated with the number of males (P = 0.045).

DISCUSSION

As predicted, the distribution of white-collared manakin leks indicates a preference for secondary growth, especially areas near abandoned pasture edges. Although not quantified, we observed more small saplings, brush, and vines in these habitats, which may provide the physical structures preferred by displaying males. The absence of leks in primary forests may be due to the lack of these physical characteristics. It is also possible that secondary forests are preferred for lek locations because the early successional vegetation provides manakins with the small fruits they eat.

Alternatively, the preference of secondary growth areas for leks may be related to the number of females present in those areas. The hotspot hypothesis suggests that males cluster in areas with certain physical characteristics that are attractive to females, allowing males increased access to potential mates (Westcott 1995). If so, the number of males per lek may be related to the number of females immediately surrounding the lek, which might explain why there are no significant differences in the number of males in each lek. An examination of female density and activity in these areas may provide more support for this hypothesis.

The mean activity per individual increased with lek size. Since most males in a white-collar manakin lek display (i.e., there are no inactive subordinates - Wray and Osterling 1995), when more males congregate together it would be expected that individuals would display even more to out-compete each other. Thus it seems that there is an optimal lek size and males would join leks that are large enough to attract females but not so big as to require a disproportionate expenditure of energy in display.

Though the factors controlling lek location are still largely unknown, white-collar manakins do show preference for specific habitat types, which suggests that the vegetative structure of available habitats influences the placement of leks.

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