Table 1: Number of each bird species by foraging guilds captured in early successional and in primary forest at La Selva, Costa Rica.

Bird species, common name	Succesional	Primary
Frugivorous species	11.8%	15.4%
Manacus candei, White-collared Manakin	4	
Pipra mentalis, Red-capped Manakin		2
Insectivorous species	11.8%	30.8%
Glyphorhynchus spirurus, Wedge-billed Woodcreeper		2
Phaenostictus mcleannani, Ocellated Antbird		1
Ramphocaenus melanurus, Long-billed Gnatwren	1	
Seiurus aurocapillus, Ovenbird	1	
Terenotriccus erythrurus, Ruddy-tailed Flycatcher		1
Xenops minutus, Plain Xenops	2	
Nectivorous species	17.6%	23.0%
Chalybura urochrysia, Red-footed Plumeleteer	2	
Phaethornis longuemareus, Little Hermit	1	1
Phaethornis superciliosus, Long-tailed Hermit	1	1
Thallurania colombica, Crowned Woodnymph		1
Threnetes ruckeri, Band-tailed Barbthroat	1	
Omnivorous species	58.8%	30.8%
Arremon aurantiirostris, Orange-billed Sparrow	1	
Cyanocompsa cyanoides, Blue-backed Grosbeak	2	
Myonectes oleagineus, Ochre-bellied Flycatcher	5	4
Hylocichla mustelina, Wood Thrush	1	
Ramphocelus passerinii, Scarlet-rumped Tanager	3	
Saltator maximus, Buff-throated Saltator	5	
Tolmomyias sulfurescens, Yellow-olive Flycatcher	1	
Turdus grayi, Clay-colored Robin	1	
Total number of species per net hour	0.29	0.15
Total number individual birds per net hour	0.63	0.25

PHYSICAL AND SOCIAL STRUCTURE OF A WHITE-COLLARED MANAKIN LEK: AN OBSERVATIONAL STUDY

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Abstract. Leks are a type of mating system in which males congregate for the sole purpose of attracting and courting females, often in elaborate displays of song and dance. We observed a lek of White-collared Manakins, Manacus candei, initiating courting displays usually consisting of hopping and wing snapping in courts in the low understory of a secondary tropical forest. We found that the 11 courts within the lek varied in shape, degree of leaf litter clearing, and number of display saplings, in contrast to previous studies that had found lek courts to be consistently oval, void of litter and containing only 2-4 saplings. We also noted that several males used a single court for their individual displays and that some males displayed higher in the trees. The lek appeared to have more males than courts, suggesting the existence of floater males who do not have their own courts. Long-term studies with marked birds would help determine the extent to which the physical structure of the courts within the lek and individual birds' behaviors relate to social structure and mating success.

Key words: display behavior, reproductive success, leks

INTRODUCTION

Ninety percent of birds are monogamous. Of the 10% of the species that are not monogamous, about 30% mate in leks, a type of communal display system in which males "congregate for the sole purpose of attracting and courting females and to which females come for mating" (Emlen and Oring 1977). Mating in such systems is polygynous; a dominance hierarchy occurs among males, with the older, more dominant male(s) copulating with the most females. Females leave the lek after copulation to rear their young alone.

Lekking seems to have evolved commonly in species where males do not care for their young, and are unable to control resources or mates, for two basic reasons. Either critical resources are superabundant and widely dispersed but undefendable due to unpredictability in space and time, or intraspecific competition makes such defense too costly (Emlen and Oring 1977). In addition sexual receptiveness in females of lekking species is staggered, while males remain sexually active for the entire breeding season, skewing the operational sex ratio (the overall population ratio of fertilizable females to sexually active males) and intensifying sexual selection. By pooling their courtship displays, males are thought to increase the number of potential mates they can attract collectively. Further, contrary to the idea that leks serve only to attract potential mates, it has been suggested that males in leks benefit by secondarily increasing vigilance against potential predators and/or sharing information about food locations. Females benefit from this type of system by having the ability to mate with the most fit males based on an already established dominance hierarchy (Emlen and Oring 1977). In other species of lekking birds, males have been shown to mate more successfully closer to the center of the lek than at the periphery.

In this study, we examined how courtship display behaviors of White-collared Manakins (Manacus candei) might vary between individuals and between display courts in a lek as an indicator of social status. White-collared Manakin leks have been described as containing between 8 and 10 display courts (Snow 1976), which are cleared out areas on the forest floor containing between two and five small saplings (Wray and Osterling 1995). The birds' display behavior is characterized by hopping between saplings and ground on the edge of the court, wing snapping, and protruding of throat feathers (Stiles and Skutch 1989). The leks occur in the understory of dense, tall secondary forests.

We examined the physical and social structure of a White-collared Manakin lek. We quantified the dimensions of a lek, the number of courts contained in the lek, the orientation and size of courts, and the number of saplings contained in courts. We also examined both display and other types of behaviors of different members of the same lek. We hoped that this information would help us to further understand how a lek functions and would elucidate the

evolutionary and environmental factors that maintain such a unique and interesting mating system.

Methods

On 14-17 February 1997, we observed the behavior of White-collared Manakins (Manacus candei) in a lek at Estación Biologica La Selva, Costa Rica. The lek was located in secondary forest, adjacent to a clearing off of the Sendero El Atajo, 30 m from its junction with Sendero Tres Rios. We visually located active courts within the lek by watching for displaying individuals and searching for the characteristic elliptical clearings used as display courts. We observed individuals in the lek for a combined total of 38 h, and observed a combined total of 375 min of display activity. We observed four general categories of bird behavior: display, flight, perching, and aggression. Similarly, we heard three distinct calls from the manakins, categorized as either snaps, buzzes or chirps. We recorded the amount of time spent by individuals in each type of behavior. We counted the number of displays for various individuals as well as the number of hops per display. Heavy rains occurred frequently during the study, which reduced the display activity of the manakins, and consequently affected the quantity of data we were able to collect.

We determined the location, length, and width of eleven courts. We approximated the areas of the courts using the formula: $\pi[(\text{length}+\text{width})/4]2$, the equation for the area of a circle with radius (length+width)/4. We also recorded the apparent number of saplings, which are used as display perches within each of these courts.

Results and Discussion

Activity levels:

Lekking activity, the period of time when displays increase in frequency throughout the lek, is highly dependent on weather conditions. During the 9.5 hours we each spent observing this lek, the males displayed for only 94 min. This display behavior never occurred in the rain, and in one instance on 16 February when it began to rain display activity immediately ceased. Wray and Osterling (1995) reported that peaks in lekking activity occurred in the morning from 08:00 to 09:00. Etemad-Green and Green (1986) found an afternoon activity peak at 14:00. We found no activity peak during the morning hours, even when it was not raining, but did observe heightened afternoon activity occurring between 13:30 and 14:30. Perhaps the intermittent rain altered the birds' normal lekking schedule. It would be useful for future studies to quantify temperature and weather in relation to lekking activity at different times of day.

Display Behavior:

Peaks in lekking activity were characterized not only by displays, but also by an increase in all types of calls (chirping, snapping, and buzzing) and in frequency of flights. During the court displays, some birds hopped on the ground in addition to jumping back and forth among vertical saplings. The hops were usually, but not always, associated with a snap of the wings. A loud buzz made by the wings sometimes marked the start or conclusion of the bird's display.

Display behavior included a variety of combinations of hops (between 2-18 sideways jumps between saplings), and clicks (between 1-18). Displays were performed either alone or coicident with other displays. We suggest that it is most advantageous for the function of the lek as a whole to have males displaying in synchrony because active, "loud" leks should be easiest to locate by females, although an individual bird might benefit more from displaying alone so that he is most noticeable. Classifying certain individuals as display initiators, display followers, or solitary displayers could provide a clue to the dominance hierarchy within the lek.

The males also display outside of the courts. We observed males displaying in trees just overhead rather than on the usual displaying court on two occasions (see Fig. 1). One such display was performed by a solitary male; the other by a pair of males hopping from perch to perch on the same group of approximately five trees. A previous study reported such tree displays as being associated with the presence of a female (Wray and Osterling 1995). We did not observe females during either of these tree displays. However, we observed a different kind of behavior in the presence of a female. Three males appeared to swarm around a female perched 2-3 m in a tree. They snapped and buzzed with their wings and then flew in a circle around her. The female flew after one of the

males (location marked on Fig. 1).

Court Appearance and Maintenance:

We calculated the total area of the lek by multiplying the maximum distance between courts in a north-south and east-west direction. Courts A and K were 100 m apart and courts C and H were 43 m apart, giving an estimated lek area of 0.43 hectares (Fig. 1). The lek contained at least 11 courts. Lek courts in this species have previously been described as elliptical (Wray and Osterling 1995); however, we found that their shape was variable and that the court margins were not distinct. The approximate shapes and orientations of the courts are shown in Fig 2. The mean area of the courts was 1.75 m2 (± 0.59 s.d.). The courts contained an average of 7.5 saplings (± 2.3 s.d.), which is more than the 2-4 saplings per court estimated by Wray and Osterling (1995), although our broader definition of a sapling included all that were within the size range of those that we observed birds using as perches. It has previously been suggested that manakins minimize energy expenditure by clearing elliptical courts that extend only as far as the peripheral saplings (Etemad-Green and Green 1986, Wray and Osterling 1995); however, we found several courts with leaf area cleared beyond the exterior saplings (B, D, and H; Fig. 2).

Display courts did not appear to be as meticulously maintained as previous studies have indicated. Etemad-Green and Green (1986) reported that one can test if a court is active by placing a leaf in its center and noting subsequent removal. We do not believe this test would be an accurate indicator of an active court because four of 11 of our study courts were at least partially covered by leaf litter (courts E, F, I and J; Fig. 2). We observed manakins displaying in all four of these courts.

Lek Structure:

Based on our qualitative observations, the White-collared Manakin lek appears to be a complex association of males that do not behave in an easily discernible manner. Males display both individually and in synchrony with other males. We observed only one male in a court at any given time. On two occasions, we observed two different males perching near the same court and alternating displays within that court. This suggests that courts are either shared or not well defended. It is also possible that "floater" males lacking their own courts display in the courts of absent males, especially since there appear to be fewer courts than birds. On several occasions, we heard more birds calling from a given direction than there were visible courts in the same direction (e.g., we heard three males SE of court F during the display peak). Future studies of lek structure would be improved by individually marking birds in order to determine the number of males in the lek and the extent of court sharing.

We do not know the extent of court defense in White-collared Manakins. Some individuals remained near the display court throughout lekking, often perching on a horizontal branch or vine near the court, whereas others left the area for 5 min or more. On two occasions during peak activity, one male chased away another that flew by his display court. This suggests that some courts may be aggressively defended. Aggressive behavior does not appear to be as prevalent during periods without displays. Males perched peacefully <10 cm from each other for up to 5 min near a court. It is likely that aggression near a court increases in the presence of females.

Clearly, a long-term study of White-collared Manakin leks is necessary to fully understand the birds' territoriality, social structure and the physical structure of the leks themselves. In the White-bearded Manakin (Manacus manacus), mating success is closely correlated with position of a court within a lek (Snow 1976). In the White-collared Manakin lek we studied, courts were not meticulously maintained, may actually be shared by more than one bird and males occasionally display outside of courts. Thus, the mating system in this species contrasts with that reported for other manakins and deserves further study.

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Fig. 1 Map of a White-collared Manakin lek at La Selva.

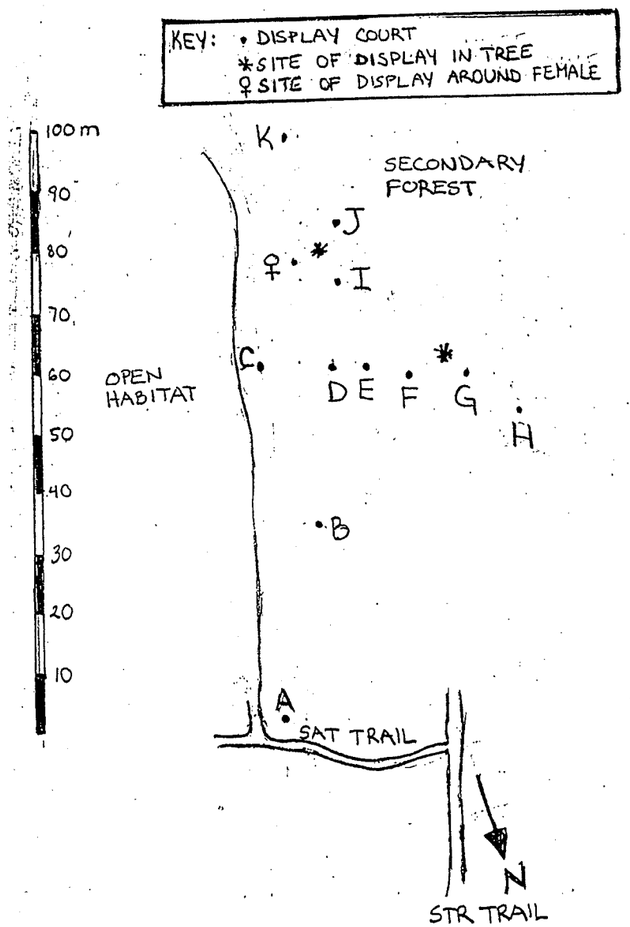
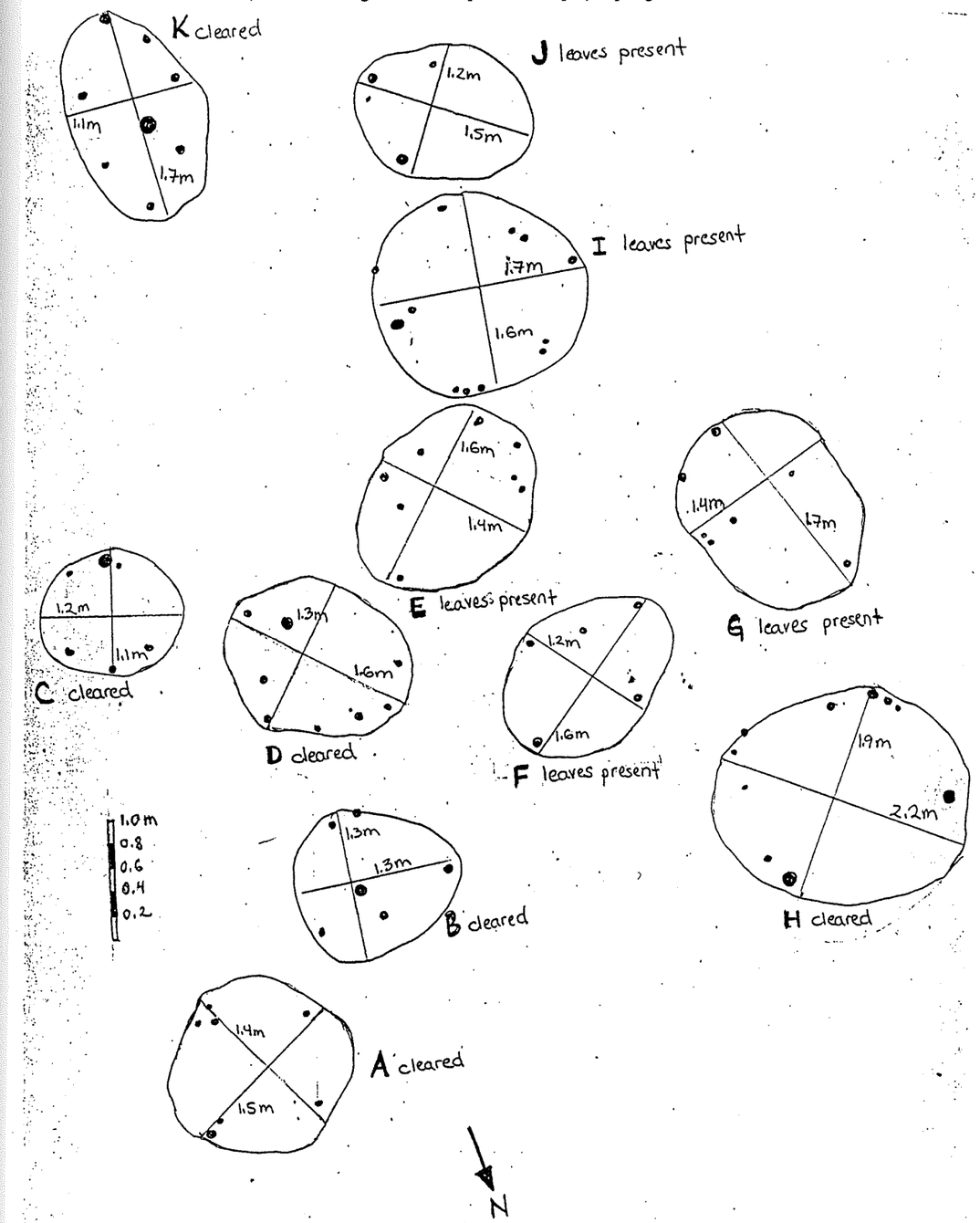
Fig. 2 The approximate shapes and orientations of eleven courts within a White-collared Manakin lek. Average court size was 1.75 m2, and the average number of potential display saplings contained within a court was 7.5.