Discussion

Habitat structure appears to influence the distribution of *D. pumilio*, with more frogs in areas with denser understory vegetation. The lack of a clear relationship between frog abundance and ant or leaf litter abundance, however, suggests that neither of these resources are limiting in the La Selva preserve, and they are unlikely to be major factors driving frog distribution.

Past research has reported multiple factors affecting *D. pumilio* distribution, including bromeliad density and calling sites (Donnelly 1989, Pröhl and Hödl 1999), indicating that habitat choice is a complex process and is determined by no single factor. Our data show that frog density is higher in the denser understories of the secondary growth, cacao, and 0 - 1 year successional forests, but very low in the primary forest. We suggest that calling sites are more available in these habitats with dense vegetation near the ground, which may contribute to the higher abundance of frogs found there. Further, we suggest that there may be a tradeoff: understory density increases the number of calling sites but also could muffle the audibility of calls. Further study may be able to better define calling sites and investigate their influence on *D. pumilio* habitat selection.

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The effects of *Manacus candei* on the vegetative composition of lekking sites

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Abstract: Manacus candei, the white collared manakin, is an avian frugivore that acts as an important seed disperser for Melostomataceae and Rubiaceae plants within La Selva Biological Reserve. We hypothesized that *M. candei* influences the vegetative structure of its habitat through seed dispersal. Since *M. candei* congregates in leks to perform communal courtship displays, we predicted that *M. candei*'s influence would be greatest at the lekking site and would be concentrated within the display courts. We predicted that the abundance of seeds and Melostomataceae and Rubiaceae plants would be greater at the display courts and within lekking sites as a whole compared to randomly chosen non-lekking site. We found significantly more seeds per unit area on manakin display plots and lekking plots than on non-lekking plots. Melostomataceae plants were proportionally most abundant at display sites and Rubiaceae plants were proportionally most abundant at lekking sites. We conclude that seeds and Melostomataceae and Rubiaceae plants are aggregated in the relatively small *M. candei* lekking area, probably due to the influence of *M. candei* . These results suggest that *M. candei* may influence the vegetative composition of this area.

Key Words: leks, manakins, seed dispersal, vegetative composition

Introduction

Manacus candei, the white collared manakin, is an avian frugivore found within La Selva Biological Reserve. Previous studies found that 95% of sampled *M. candei* feces contained seeds and/or pulp; a large proportion of these seeds belong to Melostomataceae and Rubiaceae fruits (Levey 1984, Loiselle and Blake 1990). *M candei's* mobility and feeding behavior may allow it to function as an important seed disperser. As a result, we hypothesized that *M. candei* influences the vegetative structure of its habitat through seed dispersal.

When not foraging, males congregate at lekking sites in order to perform communal courtship displays. Lekking sites are composed of a number of courts, each court dominated by a pair of males (Foster 1977). As a result of this social behavior, we predicted that *M. candei*'s influence on habitat would be greatest at the lekking site and would be concentrated within the display courts, where males spend the majority of their non-foraging time. Therefore, the abundance of seeds and the proportion of Melostomataceae and Rubiaceae plants should be greater within display courts and the surrounding lekking site than at a random non-lekking site.

Methods

We located four different *M. candei* lekking sites within La Selva Biological Reserve. Site one was at trail marker 2950 m on the Sendero Tres Rios, site two was at trail marker 1250 on the Sendero Atajo, site three was behind Cabina Tortuga, and site four was behind the laboratory building. A schematic of a study area with hypothetical plot locations is shown in Fig. 1. We established plots on all display courts that we could find within each lekking area and also established four 1 x 1 m random plots within each lekking area. In addition, we established four 1 x 1 m random plots that were between 30 and 50 m from the lekking area. We collected seeds, seedlings, and understory plants from each court and random plot. All understory seedlings and understory plants were collected, regardless of height or size. To standardize effort, both investigators collected seeds for a 4-min period at each sampled location. Seedlings and understory plants were identified as Melostomataceae, Rubiaceae, or "other". We were unable to identify seeds.

Data were analyzed with a nested ANOVA (plot type within site). Inclusion of Site 2 data caused a significant effect of site,

as it generally had lower numbers of seeds. To simplify subsequent pairwise comparisons, we excluded Site 2 as an outlier and used Tukey-Kramer HSD comparisons to determine how plot type seed abundance differed.

Results

We found a significant effect of plot type on number of seeds per plot (ANOVA, $F = 4.62$, $df = 8, 25$, $P = 0.002$; Plot type (Site): $F = 5.23$, $df = 6$, $P = 0.001$). We found more seeds on manakin display court plots (24.7 ± 6.4 seeds per plot) and the surrounding lekking plots (16.9 ± 5.6 seeds per plot) than on non-lekking plots (3.5 ± 0.9 seeds per plot) (ANOVA, $F = 15.27$, $df = 2, 31$, $P < 0.0001$; Fig. 2).

Display courts had a significantly greater proportion of Melostomataceae plants, lekking sites had a significantly greater proportion of Rubiaceae plants, and non-lekking sites had a significantly greater proportion of "other" plants than expected by chi-square analysis ($\chi^2 = 20.34$, $df = 4, 292$, $P = 0.0004$; Fig. 3).

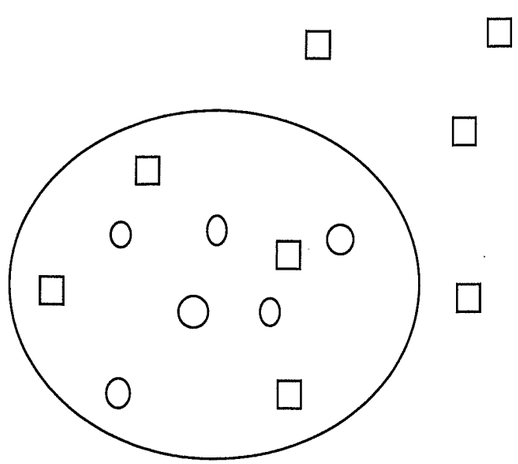

Fig 1. Schematic representation of a sample lekking site. Large circle represents the lekking site, smaller circles represent display courts, and squares represent randomly located sample plots. Location of non-lekking site random plots, squares outside of the large circle, not to scale.

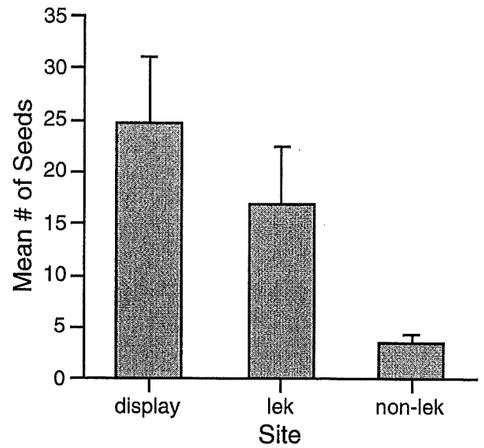

Fig. 2. Mean number of seeds (± 1 SE) found in display courts (n = 13), random lekking plots (n = 16), and random non-lekking plots (n = 16) during 4-min search intervals.

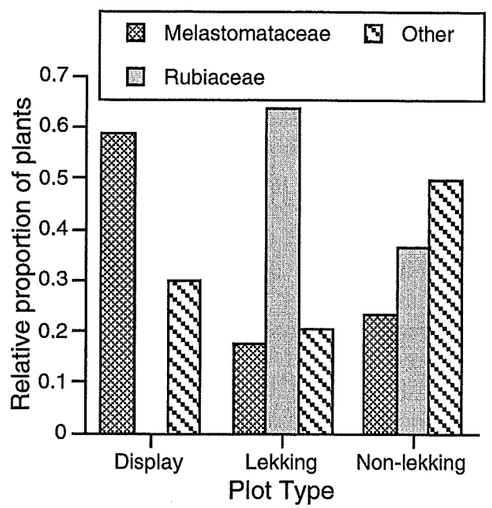

Fig. 3. Relative proportion of plant families found in display courts (n = 7), lekking plots (n = 7), and non-lekking plots (n = 7). Seedlings and understory vegetation were classified as Melastomataceae, Rubiaceae, or "other".

Discussion

Seed concentration was higher in lekking areas than in non-lekking areas (Fig. 2). As a lekking species, *M. candei* spends large amounts of time in aggregations where activity is concentrated over a small area. It follows that seeds from fruits ingested by these birds will also be aggregated in lekking sites relative to non-lekking sites, and particularly in display courts where activity is concentrated. Thus, *M. candei* may influence the vegetative composition of this area through aggregation of seeds.

Evidence of *M. candei's* influence upon the vegetative composition of its lekking area is realized in the non-random distribution of Melostomataceae and Rubiaceae plants. Loiselle and Blake's (1990) analysis of *M. candei's* fecal samples found that *M. candei* often forages on these two families of plants. If *M. candei* influences the vegetative composition of its lekking site by depositing seeds in its feces, then these two families should be found more prevalent within the lekking site than in non-lekking sites. Our results further strengthen Loiselle and Blake's (1993) suggestion that birds influence the structure of their habitat by dispersing seeds through their feeding and movement patterns.

In addition to affecting the spatial distribution of seeds, and thus vegetation, *M. candei's* may alter the abiotic conditions in which the seeds germinate. *M. candei* clears leaf litter and some ground vegetation in the lekking areas, such that the aggregated seeds may germinate in light and humidity conditions substantially different than those of the surrounding forest. Perhaps this cleared area is better suited for Melostomataceae seed germination and growth, whereas non-cleared areas facilitate germination and growth of Rubiaceae seeds, as reflected by our results for vegetative composition (Fig. 3). It is also possible that clearing of the courts by *M. candei* may disturb seed germination and growth.

Though we could not directly measure *M. candei*'s influence upon the composition of its habitat, we present evidence that strongly suggests that *M. candei* alters its habitat through changing seed abundance and plant community composition. For future studies, we would encourage the examination of taxonomic categories of seeds, seedlings, and understory vegetation in order to better assess *M. candei*'s influence on the vegetative composition of its habitat and to validate our assumption about seed germination and survival.

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