could also be that the trees have leaves with a higher leaf water content, or fruit for a longer period of time, thus offering more nutritional value to the monkeys than trees farther from the stream.

In former study Bird et. al. 1996 reported that there was no significant difference in the activity time budgets between adult males, females without young, and mothers with young. We felt that this study was inadequate and that a subsequent study was in order for several reasons: 1) the duration and time of day of this study was inconsistent, 2) data analysis suggests a high degree of variance due to differences in individual troops, sites, and activity throughout the day, and 3) the previous study analyzed observational data from a limited and unrepresentative sampling period.

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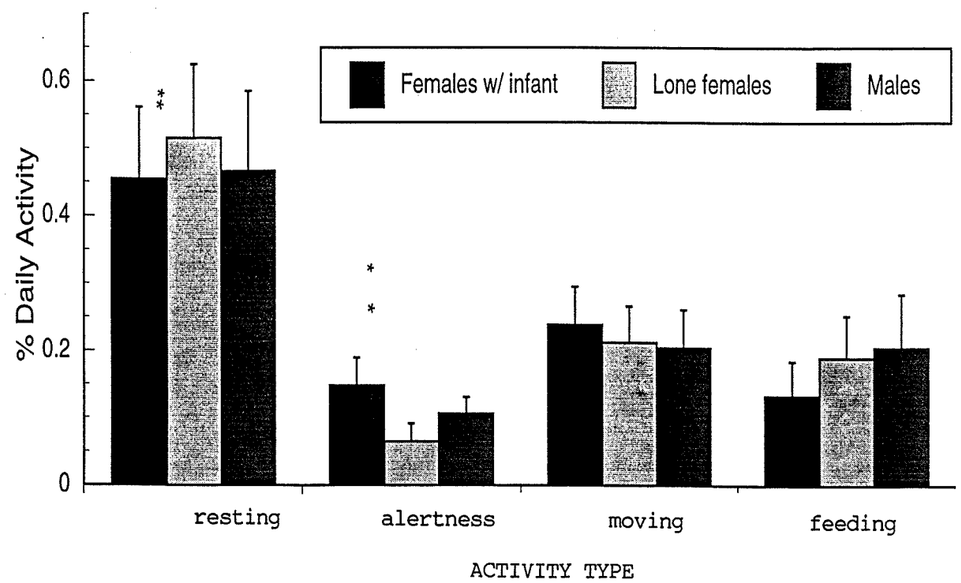

FIG.1. Comparison of average daily time allocations of three classes of A.palliata on January 14, 1997 in Palo Verde National Park. Sample size=24 monkeys. Asterisk (*) indicates statistical significance.

TERRITORIAL SITE SELECTION BY THE CARPENTER BEE *XYLOCOPA GUALANENSIS*

Karl R. Kronlein

Abstract. Male carpenter bees, *Xylocopa gualanensis*, have been observed hovering for extended periods (at least 45 min) in distinct hover sites in lowland dry forest at Palo Verde, Costa Rica. I tested whether these hover sites possessed some resource actively defended by males, possibly for attracting females. The proximity to male hovering sites of two resources, food and potential female nesting sites, were quantified. I found no significant relationships between the two resources and locations of male hover sites. However, qualitative observations of spatially clumped male hovering sites suggests an alternative hypothesis. It is possible that individual male carpenter bees achieve greater reproductive success by aggregating near other males, irrespective of local resources, because aggregations attract female bees.

Key words: carpenter bees, territorial behavior, resource defense, mating displays

Introduction

Territoriality is often observed during the mating seasons of organisms as individuals simultaneously try to attract mates and defend areas of high resource abundance. In many species, females will mate with males securing the best territories. Active defense of these territories, in the form of aggressive behaviors or vocalizations, are critical to the male's fitness.

During the dry season in Palo Verde National Wildlife Refuge, Guanacaste Province, male carpenter bees, *Xylocopa gualanensis*, were observed hovering at small stations while continually emitting a loud, audible "buzzing." Although many have observed this territorial patrolling, the behavioral significance for this behavior is unknown. It has been suggested that the hovering behavior may play a role in mating, although apparently no data exist to support this claim (Frankie et al. 1983). Regardless of the underlying causal factors, the energetic costs of the hovering behavior to the male carpenter bees indicates that hovering must benefit the males in some way.

I hypothesized that these hovering sites represent territories into which males are trying to attract females. If the hovering sites are territories, then there might be some limiting resource which the males are protecting. To test this, I assessed the availability of resources--food flowering plants and potential nest sites--near the hovering sites. Females excavate tunnels in dead trees in which they lay their eggs; therefore, the distance from male hovering sites to nearest dead tree was quantified to measure the proximity of potential nest sites. If the males are protecting a resource, then intraspecific aggression between males would be expected. I observed the behavior of individual males to determine if aggressive encounters between males were occurring. Another potential factor which might increase territorial competition between males would be territory limitation; I tested this by removing individuals and monitoring sites for re colonization.

Methods

Carpenter bees were observed on 14 January 1997 at the Palo Verde National Wildlife Refuge, Costa Rica, along the Sendero Guayacancito trail. I monitored 200 m of this path and recorded all males located within 3 m of either side of the trail.

Food availability was measured by classifying the bush containing the primary station as flowering or non-flowering. To estimate proximity to a potential female nest site, I measured the distance from the male's primary station to the nearest dead tree. To determine if dead trees were a potential cue for males in site selection, and, therefore, a potential resource for active defense, I also measured the linear distance of the nearest dead tree (DBH > 10 cm) from randomly chosen points along the transect.

Individual males were observed for 10 min. During that time, male behavior was classified into three groups: (1) time spent hovering at primary station, (2) time spent patrolling, and (3) time spent in aggressive bouts. The primary station was defined as the three dimensional area in which the individual hovered. A patrol was defined as general movement outside the primary station. If the focal bee left the primary station and chased another conspecific male in the same

location, then the occurrence was listed as an aggressive bout.

After 10 min, the focal male was captured and marked with a paint pen. Bees were then released at the same site and the site was observed for another 10 min to estimate site fidelity. After 24 hours, the sites were checked for re colonization by a marked or new male.

RESULTS

I observed 12 males, nine of which were in a 30 m stretch of the path. The hovering sites occupied a space estimated to be approximately 0.03 m3. The distance of a male hovering site to a potential nest site did not differ significantly from the distance of a randomly selected point along the transect to a potential nest site (t=0.868, df=22, P=0.394; Fig. 1). The trees in which the territories were established were of several different species, none of which were flowering at the time.

Patrolling behavior was observed in only five of the 12 males. Of those five males that patrolled, the mean number of patrols was 3 and the mean duration of individual patrols was 9 s. Two of the 12 males were observed in aggressive encounters (chasing) with non-territory holding males. Aggressive encounters in these two cases lasted approximately 10 s .

Over a two day period, no marked bees returned to their territories, nor did other bees reoccupy an abandoned territory once the resident bees were removed.

Two females were observed feeding on flowers along the path, however, the females never landed close to any male hovering sites. No feeding behavior was observed in the hovering males.

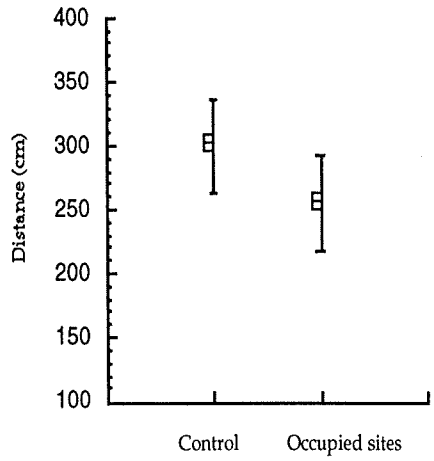

FIG. 1. A comparison of the positions of potential nesting sites relative to male territories. Potential nesting sites are defined as dead trees >10 cm DBH. For the control, distance represents the linear distance to a potential nesting site from a randomly selected point on the trail. In the occupied sites, this measurement is the linear distance between hovering individuals and potential nesting sites. The differences between mean distances is not significant.

DISCUSSION

Little is known about the mechanisms behind carpenter bee behavior (Frankie et al. 1983). Although two aggressive encounters between conspecifics were observed (suggesting potential territorial behavior), I found no patterns between the selection of territory sites and the examined surrounding resources. Therefore, the hover sites may not function as territories where resources or reproductive activities are concentrated. However, the high energy expense imposed on male carpenter bees by this behavior implies some benefit. Perhaps the behavior increases male reproductive success through some other means.

One possible explanation could be that the hover sites are for mating displays. The loud buzzing could be an auditory signal for informing females of male locations. The qualitative observation that nine of the 12 focal males were found along a 30 m stretch of the path is interesting. Clumped mating display behaviors have been documented in other organisms, such as manakins (Stiles and Skutch 1989) and mud-puddle frogs (Rand 1983). Perhaps clumping mating behavior occurs in some insects as well. By aggregating, male carpenter bees may increase their individual reproductive success by increasing the overall audible signal for females. This phenomenon and the advantages that it confers to males warrants further investigation.

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