An evaluation of community structures in the guild of vertebrates that exploit fruiting fig trees

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Abstract: A food resource that is predictable in time and space can allow for the development of a structured community that partitions the resource. In contrast, fruiting fig trees in Neotropical forests create an unpredictable and ephemeral resource. We tested for structure in the guild of species that exploit figs by observing foraging vertebrates at a fruiting fig for three consecutive days. We recorded 6 mammal species and 4 bird species foraging on figs from the tree, plus two predator species that appeared to be hunting the consumers. There was little order to the diurnal patterns of species' appearances at the tree, and there was little evidence for spatial partitioning (although there was a clear separation between canopy and ground species). There was evidence of a loose dominance hierarchy in the tree canopy, with spider monkeys tending to supplant other species. Over three days, the number of species foraging in the canopy decreased, as did interspecific interactions and the simultaneous occurrence of different species. The unpredictability of fig resources may limit the structure of vertebrate guilds that exploit figs. Nonetheless, there is a diverse community that consumes large quantities of figs in surprisingly few days.

Key Words: Ephemeral resource, Ficus lapathifolia

Introduction

Interactions between co-occurring species are frequently a result of competition for a shared resource. Over evolutionary time, competition can result in partitioning of resources in time and space among species. Such partitioning might be most likely when resource supplies are consistent or at least predictable. In Neotropical forests, mast fruiting of fig trees creates a resource that is unpredictable in time and space. All of the fruits on a single fig tree ripen simultaneously, but individual trees fruit asynchronously. When ripe, fig fruits are consumed by virtually all terrestrial vertebrates that are normally omnivorous, frugivorous or herbivorous (Janzen, 1979). Apparently, this reproductive strategy benefits fig trees by attracting an abundance of animals to consume and disperse the seeds.

It could be that the guild of species consuming figs is at least partly structured, as is the case for ant birds (Calvi et al. 2000) and many other guilds of vertebrates, or it could be that fruiting fig trees are so ephemeral and unpredictable that it precludes the development of community structure in species that utilize the resource. Structure could be manifested through a displacement hierarchy, such that the presence of one species predictably precludes another, or by a neat partitioning in time with predictable temporal patterns of segregation. Alternatively, species might exploit this resource randomly in time and space, with no associations between the presence of one species and the presence of another. We tested these hypotheses by observing a fruiting *Ficus lapathifolia* tree for three consecutive days. We evaluated patterns of association between which species came, when they were foraging and the location where they foraged.

Methods

We located a fruiting *F. lapathifolia* on 1 February 2002 in Corcovado National Park, on the Osa Peninsula of Costa Rica. The tree was approximately 50 m south of the Sirena trail in Pacific lowland tropical rainforest. It was 34.1 m tall, had an irregular diameter ranging from approximately 1 – 4 m and a crown diameter of approximately 30 m.

We observed the fig tree from 07:30 – 11:15 and from 14:20 - 17:10 on 1 February, again from 07:15 - 11:15 and from 12:15 - 17:15 on the following two days (days 2 and 3) and for 20 min on day 2 after dark. Two observers sat silently approximately 10 m from either side of the trunk and watched the tree and surrounding ground for mammals and birds. Observers recorded the location of each animal (upper, middle or lower canopy or ground), the time of arrival and departure of each animal and any behavioral interactions between species. Interactions were scored as aggressive if animals made loud calls at one another or chased each other and submissive if one animal moved away (without obvious provocation) when another approached.

We analyzed the number of species foraging using a one-way ANOVA followed by a Tukey-Kramer to test for differences among days in species present per 10 min interval.

Results

On 2 February 2002, the first day of observation, binocular scans revealed many figs on every branch, fruits fell while we observed and we smelled fig fruits up to 50 m away from the tree. It appeared that the tree had just begun to produce ripe fruit. On days 2 and 3, fruits were difficult to find on the tree with binoculars and few if any figs fell naturally from the tree.

During the three days, we recorded six mammal species and four bird species foraging on figs from this tree (Fig. 1 - 3, Appendix): Geoffroy's spider monkeys, squirrel monkeys, mantled howler monkeys, agoutis, white-nosed coatis, red brocket deer, crested guans, little tinamous, scarlet macaws and white–tipped doves. We also recorded two vertebrate predators, one mammal and one bird, that appeared to be hunting animals consuming the figs (Fig. 1 - 3): jaguarundi and common black-hawk. In an average 10 min interval, there were 1 - 2 species of vertebrate at the tree (Fig. 4). All three monkey species, agoutis and guans were sometimes present as more than one individual. There was a clear distinction between species that foraged on the ground (agouti, coati, brocket deer, tinamou and dove) vs. the canopy (spider monkey, squirrel monkey, howler monkey, guan and macaw). Ground species did not seem to partition foraging space among themselves; coatis and agoutis appeared to move at random beneath the canopy, although individual agoutis appeared to maintain some distance from any other agoutis or coatis that were present. In the canopy, guans and spider monkeys displayed a tendency for spatial partitioning. Upon arrival of spider monkeys, guans moved to the upper canopy or left the tree completely until the spider monkeys departure.

There was only limited evidence for temporal partitioning of resources among fig consumers. Spider monkeys foraged in the tree during the early morning each day and again in late afternoon during days 2 and 3 (Fig. 1 - 3). One or more agoutis were present at most times of the morning and afternoon. Other species appeared to come and go at random with respect to time of day. No foragers were observed with a powerful flashlight on day 2 between 22:30 and 23:15.

There were some patterns from day 1 to day 3. Canopy foraging decreased more from days 1 to 3 than ground foraging: animal•minutes per hour of observation = 205, 62 and 17 vs. 75, 29 and 27 for days 1 – 3 in canopy vs. ground. The average number of species present simultaneously per 10 min sampling intervals was also highest on day 1 (ANOVA, Tukey-Kramer, $F_{2, 160} = 30.0$, $P < 0.001$; Fig. 4). Furthermore, all interspecific interactions (3) occurred on day 1 of the study: a spider monkey ran shouting towards a guan, forcing it to depart from the canopy; a troop of howler monkeys exited the canopy without provocation upon the arrival of a troop of spider monkeys; an agouti ran making high pitched scream-like vocalizations to the other side of the trunk when a coati arrived. There was no indication of behavioral interactions between species foraging on the ground vs.

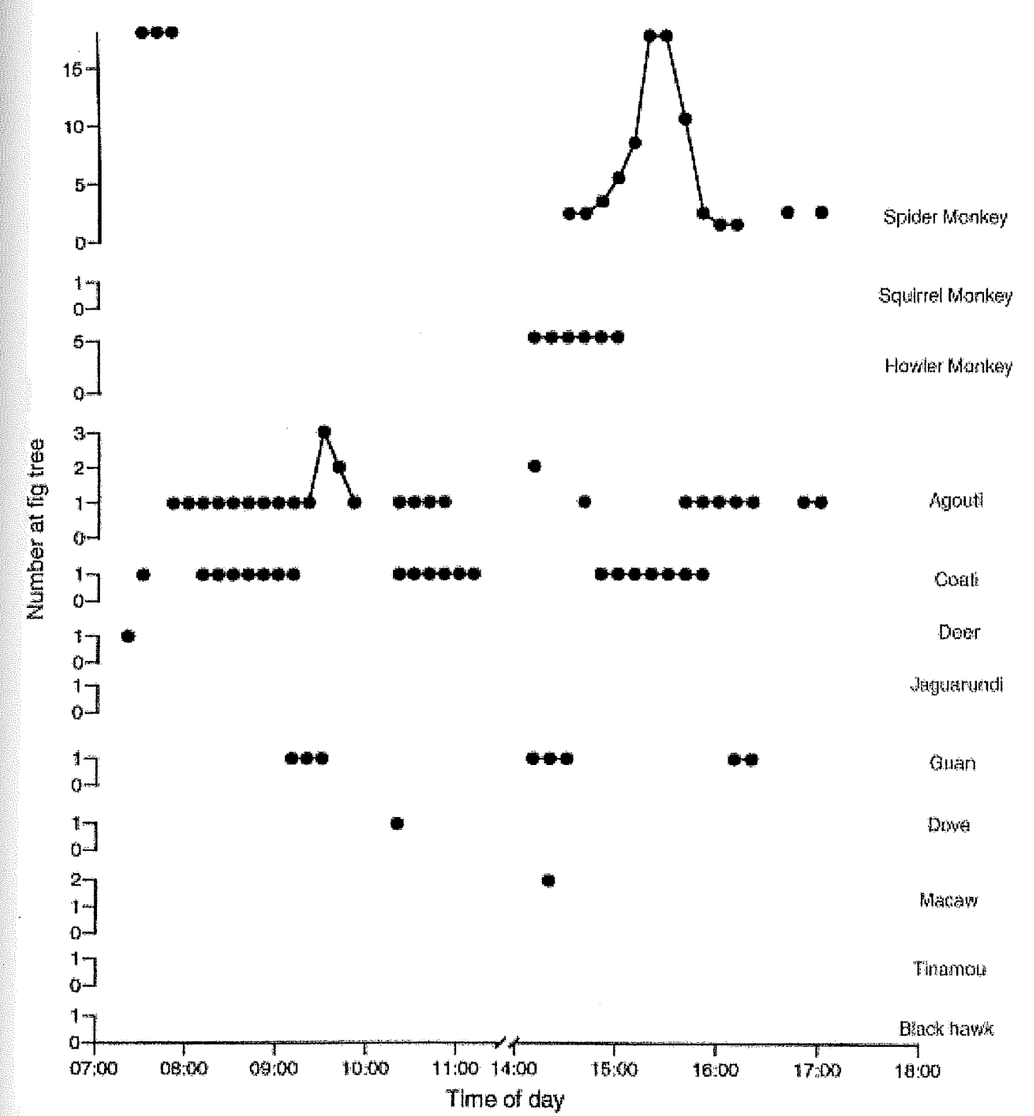

FIG. 1. Number of individuals of 12 species present at a fruiting fig tree on 2 February 2002 (day 1).

those in the tree; in fact, there were long intervals of simultaneous foraging by agoutis and guans and by agoutis and spider monkeys (Fig. 1 - 3).

Discussion

Our results revealed a diverse, but weakly structured, guild of vertebrate species exploiting fig resources. The only suggestion of a temporal pattern in fig foraging was the repeated morning arrival of spider monkeys, although this could be a result of their daily activity schedule and unrelated to partitioning fig resources. Despite the frequent presence of agoutis, there seemed to be no pattern in their foraging time over the course of the study.

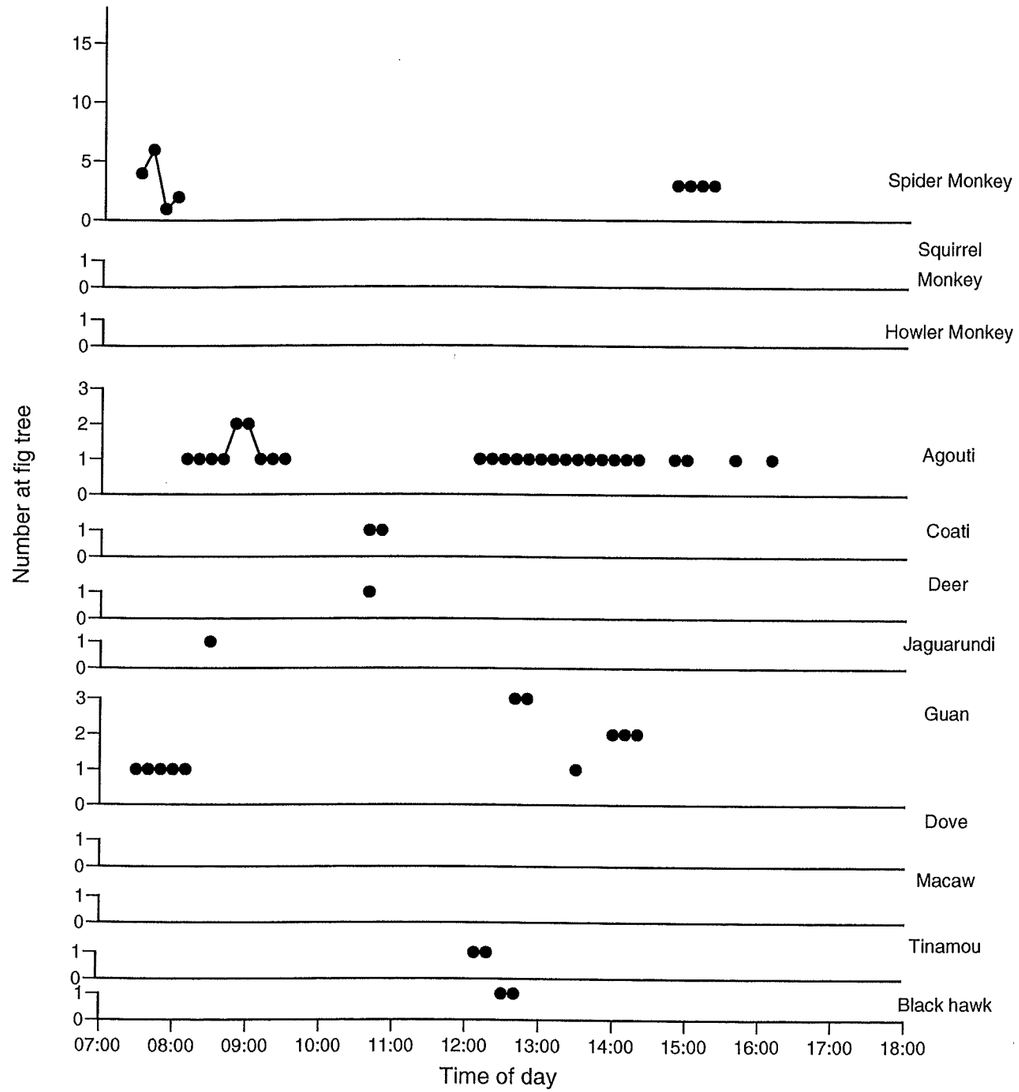

FIG 2. Number of individuals of 12 species present at a fruiting fig tree on 3 February 2002 (day 2).

The rapid reduction of figs in the canopy may have influenced guild structure. As resource availability diminished over the course of the study, so did foraging. Ground foraging declined less from day 1 – 3 than canopy foraging, presumably reflecting the accumulation of figs on the ground after they fell from the tree. The decrease in fig resources was related to a decline in behavioral interactions between species. The aggressive and submissive behaviors seen on day 1 suggest that the resource was of higher value to the foragers at that time and that spider monkeys were dominant exploiters in this system. The large troop of spider monkeys foraging at the tree on day 2 (16 individuals) indicate that the

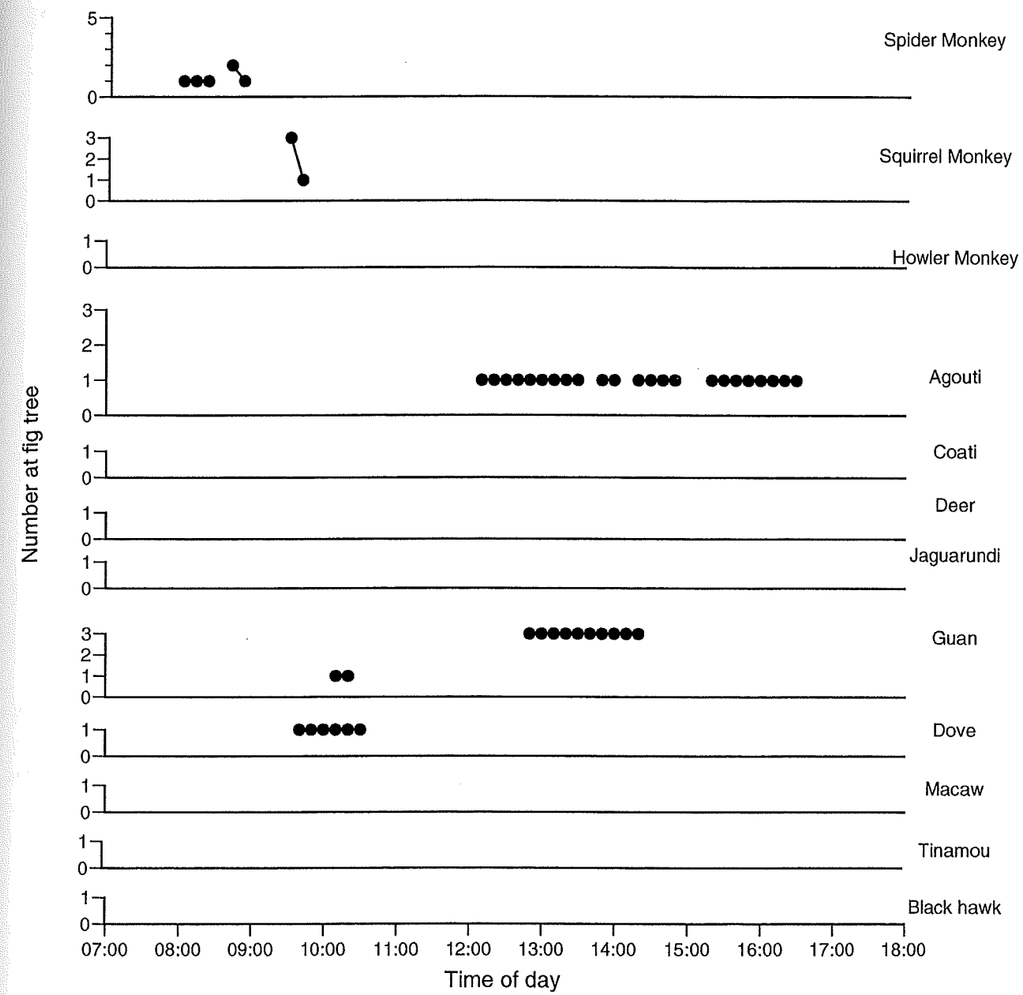

FIG. 3. Number of individuals of 12 species present at a fruiting fig tree on 4 February 2002 (day 3).

fig tree was a highly valuable food resource, as spider monkeys generally forage in groups of 2 - 4 individuals, uniting as an entire troop only to sleep or to exploit a high quality food resource (Janzen 1983).

Use of a common resource by a multi-species guild can fall anywhere along a gradient from completely unstructured (species occur at random with respect to space, time and the presence of other species) to a loose dominance hierarchy (in which some species predictably supplant others), to a highly structured system in which species are uniformly and predictably dispersed in space and time. Communities exploiting other ephemeral resources might show patterns similar to those observed at the fig tree in this study, with 1 or 2 species dominating the resource at its peak abundance and a decrease in activity and interspecific interactions as the abundance decreases. Still others could fall elsewhere along the gradient of resource partitioning. For ex-

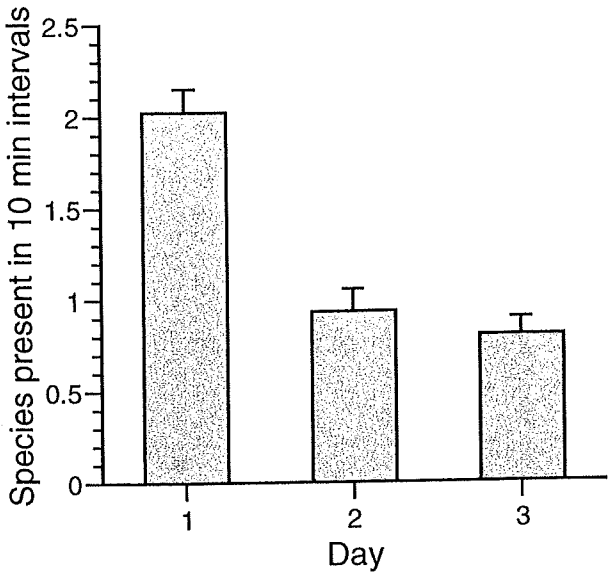

FIG. 4. The average number of species present per 10 min interval at a fruiting *Ficus lapathifolia* over 3 days (+ SE).

ample, when a population of trees fruits synchronously, such as during an oak mast, resources may be so overabundant that there is no selection for partitioning the resource and, therefore, no patterns in time or space would exist. With smaller, more ephemeral resources, like carrion, there might be a tendency for well-developed dominance hierarchies, with some species being efficient at locating unexploited resources and others being effective at dominating resource patches already occupied by the species. It seems possible that the extent and type of community structure varies with the size, quality, longevity and predictability of resources. As communities become more structured, it seems likely that overall resource use efficiency increases, thus permitting the coexistence of a more diverse assemblage of species.

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APPENDIX. Vertebrate foraging at a fruiting fig tree *(Ficus lapathifola)* in Corcovado National Park on 1 - 3 Februrary, 2002.

Common name	Scientific name
Agouti	*Dasyprocta punctata*
Common Black-hawk	*Buteogallus anthracinus*
Geoffroy' s Spider Monkey	*Ateles geoffroyi*
Crested Guan	*Penelope purpurascens*
Jaguarundi	*Herpailurus yaguarondi*
Little Tinamou	*Crypturellus soui*
Mantled Howler Monkey	*Alouatta palliata*
Red Brocket Deer	*Mazama americana*
Scarlet Macaw	*Ara macao*
Squirrel Monkey	*Saimiri oerstedii*
White-nosed Coati	*Nasua narica*
White-tipped Dove	*Leptotila verreauxi*