SYNCHRONOUS FRUITING IN *DIPTERYX PANAMENSIS* AND THE RELATIVE ROLES OF SEED PREDATORS AND DISPERSERS

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Abstract: Dipteryx panamensis, a large emergent tree at La Selva biological station, displays temporally synchronous fruiting among trees. The relative roles of seed predators and dispersers likely influence the spatial scale at which synchronous fruiting occurs. We evaluated the relative roles of fruit and seed consumers, as well as spatial patterns of fruiting and non-fruiting trees, with the hypothesis that the scale of synchronous fruiting would reflect the identity of the predominant seed predator or disperser. Almost all seed movement occurred on the ground, and synchronous fruiting occurred at the small scale of tree clusters, suggesting that ground seed consumers like rodents are the dominant drivers of patterns in the synchronous fruiting of *D. panamensis*.

Key words: agouti, emergent tree, great green macaw, masting

INTRODUCTION

Dipteryx panamensis (Fabaceae) produces very large seeds covered by a thick, hard shell and fleshy fruit, which attract a number of large vertebrate dispersers and seed predators. At La Selva Biological Station, many *Dipteryx* trees seem to fruit simultaneously, which could be an adaptive strategy in two ways: more seed dispersers could be attracted to a large patch of fruiting trees and/or mass fruit production could swamp seed predators.

The spatial scale of fruiting synchrony may be determined by the relative importance of different seed dispersers and predators (i.e., which animals have the greatest positive or negative impact on seed dispersal). If wide-ranging predators such as great green macaws (*Ara ambigua*) are the most important animal species in this system, then *Dipteryx* trees should display large-scale synchrony in order to swamp the macaws with an overabundance of seeds. Small-scale or no synchrony would be an ineffective strategy against macaws because the birds could easily locate small fruiting patches or lone individuals and would exploit those trees exclusively. However, if wide-ranging dispersers such as toucans or bats are the important species, then local *Dipteryx* trees should show little or no temporal synchrony in fruit production. Far-flying birds and bats would be able to locate lone trees (especially since most reproducing *Dipteryx* are very large emergents), so synchronous fruit production would not necessarily attract any more dispersers; in fact, providing too many seeds at once would reduce the number of dispersers per tree.

Terrestrial vertebrates, unlike animals consuming fruit and seeds in the canopy, can act as both dispersers and predators, mostly through the scatterhoarding behavior of such animals as agoutis (Guariguata et al. 2002). These and other rodents are capable of cracking the *Dipteryx* shell and eating the seed, but they also cache uneaten seeds (scatterhoarding), which can facilitate dispersal. If these terrestrial animals, which are not as far-ranging as birds and bats, are most important for *Dipteryx*, then the trees should display small-scale synchrony. This strategy will both attract larger numbers of potential terrestrial dispersers and induce more scatterhoarding behavior (Guariguata et al. 2002), because the animals would have *Dipteryx* seeds only during a limited time each year. Large-scale synchrony would be less effective in this case because dispersers would be swamped

and would not be attracted to particular trees; no synchrony would be ineffective at attracting dispersers and inducing scatterhoarding behavior.

To test alternative hypotheses regarding the seed dispersal strategies of *Dipteryx*, we examined the distribution of fruiting and non-fruiting *Dipteryx* in the La Selva forest and observed the prevalence and activities of different types of seed dispersers and predators. We hypothesized that the spatial scale of fruiting synchrony would be determined by the identity of the major disperser or predator, as predicted above.

METHODS

To determine spatial distribution and fruiting synchrony of *Dipteryx* trees at La Selva, we haphazardly walked trails (primarily CCC, CCL, SUR, SOR, STR, and LOC) and recorded the location and fruiting state of all large *Dipteryx* seen. We spent a total of 20 hours observing fruiting trees for the presence of frugivorous animals (both seed dispersers and predators). For all animals seen, we recorded time spent at the tree, and made notes on foraging behavior, including number of fruits or seeds consumed.

At two fruiting trees, we recorded the number of cracked nuts, whole nuts, chewed fruits, and intact fruits in 2 x 2 m plots located every 5 m along 30 m transects (four at one tree, three at the other) beginning at the base of each tree. On each transect, we also noted the distance of the canopy edge from the base of the trunk. At these same two trees, we marked all fallen fruits in four 3 x 3 m plots located haphazardly in areas of high fruit density underneath the canopy, and recorded the number of chewed fruits and intact fruits in each plot. After 72 hours for Tree 1 and 48 hours for Tree 2, we returned to the plots and counted all marked fruits and new fruits in each plot.

RESULTS

Spatial distribution patterns of fruiting trees

We located 16 fruiting *Dipteryx* trees and 11 non-fruiting trees. Near the trails we surveyed, there appeared to be three local clusters of fruiting trees (i.e., at least three fruiting trees within a 200 m radius). We found some non-fruiting trees near but not within the fruiting clusters (Fig. 1).

Number and distribution of fallen fruits/seeds

Ground fruits were most dense directly underneath the canopy for both trees. Tree 1 showed higher density of fallen fruits underneath the outer canopy, while fruit density was highest near the trunk of Tree 2 (Table 1).

Observations of canopy feeding animals

We recorded two bird and two mammal species feeding on the fruits of *Dipteryx*. We observed one group of six great green macaws in a fruiting *Dipteryx* for 20 minutes, but did not directly witness any feeding events. The birds were eventually displaced by a group of spider monkeys (see below). Another group of four macaws was seen perched in the crown of a fruiting *Dipteryx* for 5 minutes; this group was not feeding. All other macaw sightings were of two to six birds flying over the canopy.

A group of eight spider monkeys fed actively for 30 minutes on *Dipteryx* fruit. Usually, they tasted a fruit briefly before dropping it, but occasionally (every 10 - 20 fruits) they spent several minutes eating a single fruit before dropping the intact seed. A group of six white-faced capuchins fed for 20 minutes in the same tree the following afternoon, displaying the same foraging behavior as the spider monkeys.

We observed two groups of six chestnut-mandibled toucans (*Ramphastos swainsonii*) in fruiting *Dipteryx* trees for 20 - 30 minutes each. The birds appeared mostly to be interacting so-

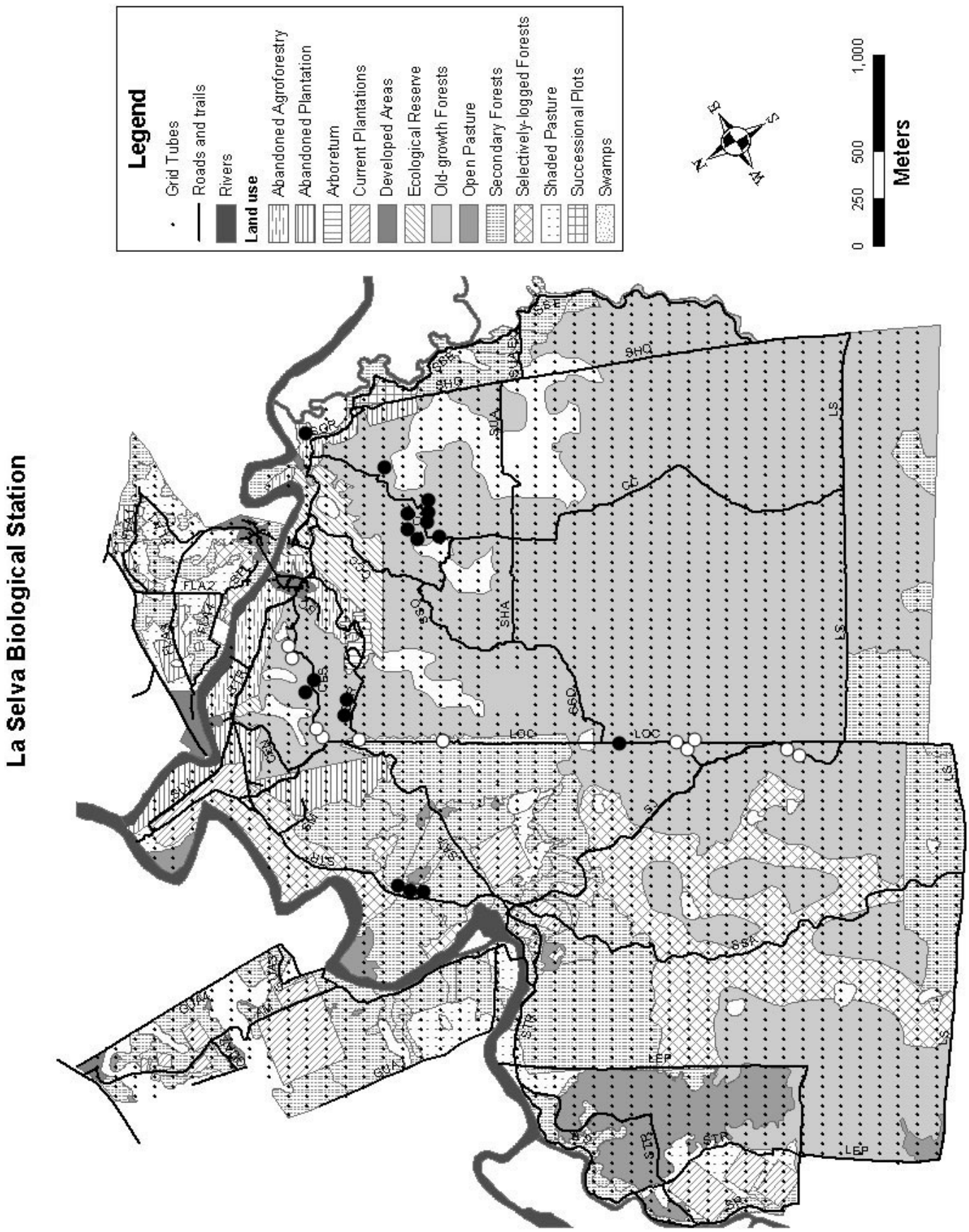

Figure 1. Distribution of fruiting (closed circles) and non-fruiting (open circles) trees of the species *Dipteryx panamensis* in La Selva Biological Station, Costa Rica.

cially and not feeding, though we did observe one toucan swallow a whole *Dipteryx* fruit. Other potential fruit-eating species observed in *Dipteryx* were two collared aracaris (*Pteroglossus torquatus*), three montezuma oropendolas (*Psarcolius montezuma*) and three parakeets (unidentified species), though none of these birds were feeding. Brief nocturnal observations (0140 - 0210) revealed a small, unidentified mammal species in the canopy and several bats flying overhead, none of which were seen to be feeding on fruits, though there was a high number of fruits dropping from the trees.

Table 1. Average number of fallen *Dipteryx* fruits/seeds found in 2 x 2 m plots at six distances from the trunk (n = 4 plots at each distance for Tree 1; n = 3 for Tree 2). Samples estimated fruit density within concentric rings of width 5 m. Average canopy radius for Tree 1 = 21.8 m, Tree 2 = 13.3 m.

Radial distance (m)	Average fruits/plot	Area of ring (m^2)	Calculated total fruits
Tree 1			
25 - 30	2	864	432
20 - 25	8	707	1413
15 - 20	29	550	4018
10 - 15	34	393	3287
5 - 10	16	236	942
0 - 5	14	79	274
		Total =	*10366*
Tree 2			
25 - 30	1	864	144
20 - 25	1	707	118
15 - 20	5	550	687
10 - 15	6	393	589
5 - 10	13	236	785
0 - 5	47	79	916
		Total =	*3239*

Marked seed plots

42 of 187 marked seeds (24%) had been removed from the plots after 72 hours at Tree 1; nine of 152 seeds (8%) had been removed after 48 hours at Tree 2. For both trees combined, 13% (39 of 302) of fruits that were initially chewed were removed, while 32% (12 of 37) of intact fruits were removed. Brief scans of the ground immediately surrounding the plots did not reveal any marked fruits.

DISCUSSION

Our results suggest small scale synchrony in the fruiting of *Dipteryx panamensis.* This is consistent with the hypothesis that ground dispersers like agoutis are driving the system. This was further supported by our high measure of ground seed removal (4 - 8% per day) relative to few observations of dispersal or predation by canopy feeders. However, this does not necessarily mean that other dispersers are unimportant. It is quite possible that dispersal by nocturnal canopy animals is common, but was overlooked due to limitations in our ability to observe them. Birds may be quite important even with few dispersal events, because the distances which they transport seeds is probably much larger than with ground dispersers and the likelihood of the seed being eaten after initial dispersal may be lower. The importance of dispersal by gravity should also not be ruled out completely. Low probability events such as ricocheting off high branches or rolling down hills may impact surprisingly many seeds given that there can be tens of thousands of fruits dropped by a tree (Table 1).

Since ground dispersers are focusing on the seed, it is curious that the seeds are surrounded by an edible flesh. Perhaps the fruit is there only to attract dispersers through the smell of the rotting fruit, or perhaps the fruit adds meaningfully to the rewards of animals

that eat the seed also. However, it is also possible that *Dipteryx* retains the fruit as an attractant to alternative dispersers. This would serve as a bet-hedging strategy, which may be especially important in such a long-lived species where abundances of specific dispersers or predators may vary drastically even within an individual tree's lifetime (> 1000 years). In fact, it is likely that the dispersal strategy of *Dipteryx* may have originally evolved in response to extinct megafauna (e.g., gomphotheres, Janzen 1982) and that some of the contemporary dispersers are attracted to the fruits only by accident.

Ideally, studies of seed dispersal should be carried out throughout the entire fruiting season and the fates of individual seeds determined. Also, all *Dipteryx* trees in a sector of forest should be mapped and monitored for multiple years to yield a detailed picture of spatial patterns in fruiting. Our short-term study suggests that, although multiple strategies may be important, the seed dispersal strategy of *Dipteryx* is presently best suited to ground dispersers.

Literature Cited

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