Effect of consumption and maturation on the abundance of ripe fruits on *Hamelia patens*

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Abstract: We examined the effects of fruit maturation and consumption on the abundance of ripe fruits on *Hamelia patens*. We monitored the maturation rates of fruits on three sample inflorescences and estimated the total number of ripe and unripe fruits on each of 10 trees. We observed bird activity on each tree for two mornings and noted number of ripe and unripe fruits consumed. Number of ripe fruits decreased during the day due to bird foraging and increased at night due to ripening and decreased bird activity. Fruits were consumed throughout the day, with a peak in consumption in the afternoon. We found that the abundance of ripe fruits remained fairly stable over the three-day observation period, an effective strategy for continuously attracting seed dispersers.

Key Words: bird foraging, Hamelia patens, *Rubiaceae, seed dispersal*

INTRODUCTION

We examined the relationship between a small neotropical tree, *Hamelia patens* (Rubiaceae) and the birds that consume its fruit. This tree flowers and fruits most of the year, and its fruits, which take about one month to mature (Croat 1978), are eaten by nine species of birds including toucans, flycatchers, thrushes, warblers, honeycreepers and tanagers (Leck 1972).

We hypothesized that the number of ripe fruits available on a tree would change predictably over the daily cycle. We predicted that there would be a net increase in the number of ripe fruits overnight due to ripening and absence of bird activity, and a net decrease in the number of ripe fruits available during the day, because of increased bird foraging.

METHODS

We conducted our study on fruiting *H. patens* near the laboratory buildings and bridge at La Selva Biological Station, Costa Rica. We counted the number of ripe fruits on each of ten trees at 06:00, 09:00 13:00, and 15:00, over a monitoring period starting at 13:00 on 15 February and ending at 6:00 on 18 February 2003. Thus, we censused the abundance of ripe fruits on each tree 11 times over 4 days. In the first census, we also estimated the number of green fruits on each tree. To monitor fruit ripening, we flagged three fruiting inflorescences on each tree and at each census time recorded the number of flowers/fruits in each of five categories: flower, small red fruit, green fruit, yellow fruit and large red (ripe) fruit.

In addition, each member of the group observed bird activity at a cluster of two or three of the census trees for 2.5 hours per day, starting immediately after the 06:00 fruit census and ending at the 09:00 census time. For each bird that perched in a sample tree, we identified the species and recorded the number of fruits, ripe or unripe, that it consumed.

RESULTS

The abundance of ripe fruits changed through the day as fruits matured and as birds consumed them (Fig. 1). Trees with greater overall fruit abundance experienced a slight increase in number of ripe fruits over the three day observation period, while trees with low fruit abundance maintained a steady cycle of nightly increase and daily decline (Fig. 2). Abundance of ripe fruits was variable among days, and we found no significant difference in mean number of ripe fruits at different times of day ($F = 0.63$, $df = 3, 106$, $P = 0.60$). Abundance of ripe

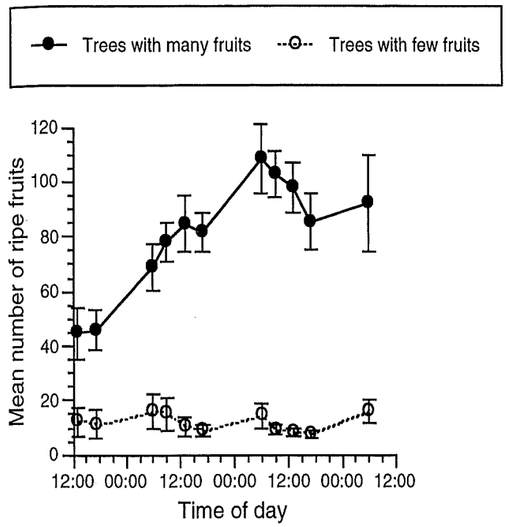

FIG. 1. Abundance of ripe fruits (mean ± SE) on *H. patens* trees with many fruits (n = 5) and trees with fewer (n = 5) over a 3-day observation period at La Selva Biological Station, Costa Rica.

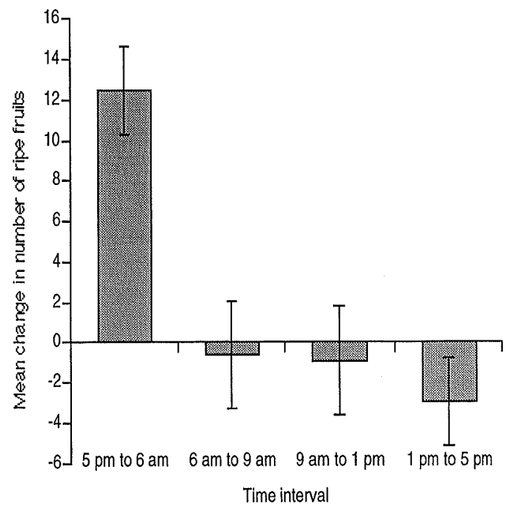

FIG. 2. The change in abundance (mean + SE) of ripe fruits on *H. patens* trees (n = 10) between censuses taken at four times per day during a three-day observation period. The overnight change was significantly different from changes during daytime measurements ($F = 10.00$, $df = 3, 96$, $P < 0.0001$).

fruits increased 12.5 ± 3.0 (mean ± SE) fruits per day overnight and decreased by 6.1 ± 3.7 (mean ± SE) fruits during the day ($F = 15.29$, $df = 1, 48$, $P < 0.001$). Fruit abundance decreased the most in the afternoon, between 13:00 and 17:00 (Fig. 2).

The proportion of unripe to ripe fruits was very high (Fig. 3). The numbers in each category (flowers, small red fruits, green fruits, yellow fruits and red fruits) on the observed inflorescences was relatively constant. However, there were roughly twice as many flowers as ripe fruits, and twice as many ripe fruits as yellow fruits. Little red fruits (semi-mature) decreased over time and green fruits (new fruits from fertilized flowers) increased. The fruits spent most of their development time green and the least time yellow.

Fruits were eaten by birds throughout the day, but there was a slight peak in fruit consumption in the afternoon. Bird foraging activity level varied greatly across sites, from 0 to 70 fruits eaten per day. We observed Black-cowled Orioles, tanagers, warblers, Clay-colored Robins, and flycatch-

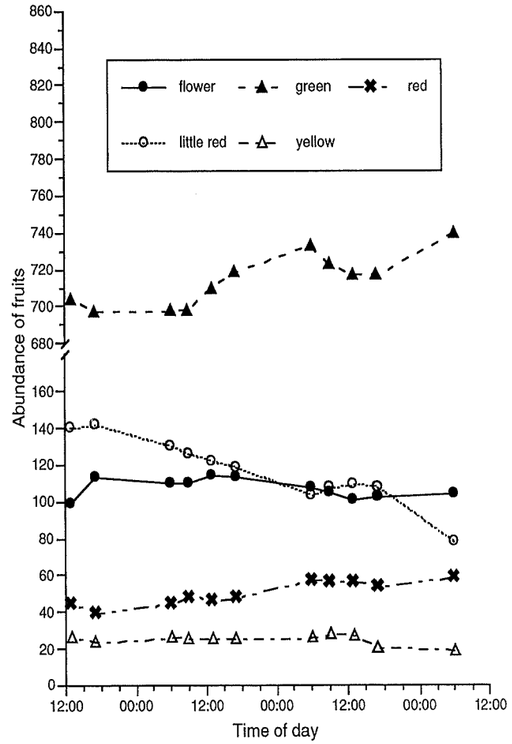

FIG. 3. Change in abundance of fruits of *H. patens* at different stages of maturity over a three-day observation period. Data represent means from three inflorescences at 10 trees at La Selva Biological Station, Costa Rica.

ers visiting the trees. Qualitatively, we observed that larger birds (Clay-colored Robins, Black-cowled Orioles, and flycatchers) ate more fruits than smaller birds (warblers and tanagers). A few green fruits were consumed by Olive Tanagers, probably before the seeds were viable.

Discussion

The number of ripe fruits on the *H. patens* tree increased overnight and decreased during the day, supporting our prediction that fruits ripen continuously. The change observed overnight represents the ripening rate because only diurnal birds consume the fruit (Leck 1972). In contrast, the change during the day represents the difference between fruit ripened and fruit eaten. Therefore, during the day birds eat fruit faster than the fruit ripens.

We expected higher bird foraging activity in the morning, but activity was patchy in space and time. Such variability in foraging activity suggests that fruit availability on these trees may not be the primary factor driving patterns in bird foraging behavior. The high variability in bird visitation that we observed may also be explained by the sporadic movements of the mixed species flocks that comprised the majority of visitors.

Although February is the month of lowest fruit production (Newstrom 1994), there were ripe fruits on all of our trees. More fruits were eaten on trees with more ripe fruits. At trees with many ripe fruits, we observed that more birds visited and individual birds foraged longer.

Contrary to our second prediction, there was a slight net increase of about six ripe fruits per tree per day over the sample period. However, we did not test this statistically, and the number of ripe fruits on a tree was relatively stable over time (Fig. 3).

We were able to observe the ripening of fruits through various stages over a three-day period. There were far more unripe than ripe fruits on all trees, because fruits spend most of their time in an immature state. We saw few green fruits turn yellow, but most fruits that were initially yellow had fully ripened and turned red by the end of our observations. Flowering in every month, together with a one month ripening period (Croat 1978), allows *H. patens* trees to supply ripe fruits continuously to the birds that consume them. This helps ensure that the tree does not swamp dispersers. If the tree produces too many fruits at one time, birds may stay at the tree longer and defecate more of the seeds directly under the parent, rather than dispersing them. On the other hand, if a tree does not consistently produce enough fruits to attract dispersers, birds may not visit on a regular basis and fruits may not be eaten and dispersed.

Plants must supply enough fruit to attract dispersers but not so much that fruits go uneaten and energy is wasted. We observed a variety of bird species consistently returning to *H. patens*, suggesting that the species is producing fruit fast enough to maintain reliable seed dispersers.

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