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Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs

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Abstract We describe fruiting characteristics for 12 species in a community of strangler figs (Moraceae: Urostigma) studied in Panama. We quantify diurnal and nocturnal removal rates and proportions of fruits removed, and relate them to the activities of the main dispersers of the figs: bats and birds. These results combined with previous studies show that there are clear differences between fig species with fruit that ripen red and those with fruit that remain green(ish). In the red-fruited species, the fruit are small, ripen asynchronously over relatively long periods, produce little scent, and are mainly taken during the day by birds. In contrast, in the green(ish)-fruited species, the fruits are larger, span a range of sizes, ripen relatively synchronously, produce very distinctive aromas, and are mainly taken at night by bats. This dichotomy in fruiting characteristics suggests coadaptive links between groups of dispersers and different species within the genus *Ficus*. All fig species produce a range of fruit crop sizes (10–155 fruits/m² canopy area) of which a high proportion were removed by seed dispersers (>80%). Removal rates (fruit removed per day) were positively correlated with crop size, suggesting that trees with large crop size attract more frugivores. Removal rates of green-fruited figs were significantly lower and persistence and abortion of ripe fruit were significantly higher around full moon, apparently due to the reduced activity of bats. We further estimate the number of bats that are sustained by a tree fruit crop and account for the observed fruit removal. We then discuss the evidence for coadaptation between different groups of figs and their seed dispersers. Finally, we con-

sider the conservation implications for figs as keystone resources in tropical forests.

Key words *Ficus* · Frugivory · Fruit removal · Seed dispersal · Bats · Birds · Coadaptation

Introduction

Although *Ficus* are perhaps best known for the intricate mutualism with their generally species-specific wasp pollinators (Corner 1940; Galil and Eisikowitch 1968; Ramirez 1969; Janzen 1979; Herre 1996), the ripe fruit that is one product of that interaction also provides an important food source for a wide range of frugivores that, in turn, usually disperse the viable fig seeds. The perception that *Ficus* species constitute important “keystone” resources for many frugivore groups has been supported by many authors working in many different tropical regions (Corner 1940; Janzen 1979; Foster 1982; Milton et al. 1982; Leighton and Leighton 1983; Terborgh 1986; McKey 1989; Windsor et al. 1989; Lambert and Marshall, 1991; Wrangham et al. 1993; Herre 1996; O’Brien et al. 1998; but see Gautier-Hion and Michaloud 1989; Levey et al. 1994; Goodman et al. 1997).

However, despite the importance of figs for many tropical frugivores, the details of the relationships between different components of the frugivore/seed disperser guilds and different fig species are unclear and bear on the general question of specificity and coadaptation between hosts and frugivores (Howe 1993; Herrera 1998; Levey and Benkman 1999). In particular, the factors affecting the removal of fig fruits (e.g., crop size and fruit characteristics) are less well known. Published accounts of fruit production in figs and their associations with their dispersers have thus far focused mainly on individual trees (Breitwisch 1983; Jordano 1983; Scott and Martin 1984; Goodman et al. 1997) or on individuals of one or two species of figs (August 1981; Bronstein and Hoffmann 1987; Compton et al. 1996). Furthermore, the majority of studies have been limited to diurnal removal

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of fruits. Although previous studies suggest that the New World strangling figs separate into two groups, one that primarily attracts bats, and another that primarily attracts birds (Herre 1996; Kalko et al. 1996b), quantitative as well as qualitative assessments comparing the relative importance of diurnal and nocturnal removal rates are still lacking. Moreover, few studies have addressed differences in the host-frugivore interaction across a suite of congeneric fruiting trees and their associated community of frugivores (e.g., Wheelwright 1985).

Here, we describe the fruiting characteristics of 12 fig species from a community of strangler figs (*Ficus*: Moraceae, section *Urostigma*, americana) growing in the vicinity of the Panama Canal and the interactions with their main dispersers. By using both detailed focal branch sampling in conjunction with whole-tree estimates, we compare crop size, diurnal and nocturnal fruit removal rates, proportion of fruit removed, and species composition of frugivores across a suite of congeneric fig species growing in one site. Furthermore, we use these data to assess the effect of various factors on fruit removal. For example, some authors (Howe and DeSteven 1979; Howe and Vande Kerckhove 1979; Murray 1987; Gryj and Dominguez 1996; but see Fleming 1981), report that there is a positive relationship between crop size and number of individual frugivores attracted, resulting in increased fruit removal. Finally, using published information on the dietary requirements of bats, we estimate the number that feed on the ripe fruits of a fig tree and disperse its seeds to assess the relative importance of figs as a keystone resource.

Materials and methods

Study site

The study was conducted at the Barro Colorado Nature Monument (BCNM), situated in Lake Gatun, Panama Canal (9°09' N, 79°51'

W). BCNM is covered with tropical moist, semideciduous lowland forest (Foster and Brokaw 1982). The climate is seasonal with a 3- to 4-month dry period usually between December and April (see Leigh et al. 1982). Annual rainfall totals about 260 cm with roughly 90% of it occurring during the months of the wet season.

Study trees

Fifty-three individual trees from 12 species of strangler figs in the BCNM were observed for fruit production and fruit removal for the 9 months between September 1996 and April 1997, a period that corresponds to the last 3 months of one wet season through the dry season to the beginning of the next wet season (Croat 1978; Herre 1989; Windsor et al. 1989). Nine species produce green fruit and three species, red fruit (Table 1). To ensure accessibility of individual branches for marking and detailed observations, we selected strangler figs along the shoreline of the BCNM that were easily monitored by boat.

We estimated canopy area and the cross-sectional areas of the trunk at breast height (ABH). In the frequently observed case of multiple roots, we summed ABH for all roots. In the case of trunks with large buttresses, ABH was measured above them. We estimated the crown area by stretching a tape measure from the trunk to the edge of the crown along four rays. The mean radius was then used to calculate a circular projected area.

For each tree, branches were divided into three categories: main branches, secondary branches, and small branches with fruits. The total number of main branches was counted for each tree. The number of secondary and small branches was estimated by counting them on a minimum of six main branches. The number of fruits per branch was assessed by counting them on 30 small, randomly chosen, fruit-bearing branches. Crop size was estimated as number of main branches times average number of secondary branches times average number of small branches times average number of fruits per branch.

Observations on the fruiting trees

Between fruiting episodes, each tree was surveyed every 2 weeks in order to detect the onset of fruiting cycles. From the onset of the fruiting cycle until the onset of fruit ripening, trees were followed in 2- to 3-day intervals. Five to seven focal, medium-sized branches were tagged haphazardly in different parts of the accessible crown and the number of fruits was counted for each branch. In case fruits were aborted before ripening (usually due to lack of

Table 1 Characteristics of the Panamanian fig trees. Results are presented as means±S.D. Values in parentheses present crop sample size (ABH cross-sectional areas of the trunk at breast height)

Species<	Fruit mass (g)	Fruit size (mm)	Crop size	ABH (m ²)	Canopy area (m ²)	Synchrony (%)	Persistence of ripening (days)
Green figs							
<i>Ficus citrifolia</i> (11)	1.4±0.3	15.3±1.2	9665±7001	0.02±0.01	97±45	85.8±9.7	5.6±0.5
<i>F. bullenei</i> (4)	1.6±0.3	16.5±1.5	4325±6145	0.08±0.07	103±76	85.5±9.2	6.1±0.8
<i>F. paraensis</i> (3)	1.7±0.1	17.3±0.3	2400±1153	0.02±0.01	67±76	83.3±11.9	5.3±0.6
<i>F. dugandii</i> (3)	1.7±0.3	16.9±0.6	40033±14533	0.48±0.22	670±99	87.8±19.0	4.5±0.7
<i>F. popenoei</i> (5)	3.8±0.3	23.9±0.5	8740±818	0.19±0.11	201±146	60.0±10.5	6.6±0.9
<i>F. 'near trigonata'</i> (3)	6.2±2.2	25.3±2.3	4760±5109	0.18±0.16	181±147	70.9±16.9	9.7±4.1
<i>F. trigonata</i> (4)	6.7±1.4	26.3±1.5	4350±2969	0.26±0.12	246±132	74.3±13.2	4.7±0.6
<i>F. nymphifolia</i> (5)	7.5±0.5	28.2±1.3	3689±4409	0.10±0.09	111±50	84.6±6.7	8.0±0.8
<i>F. obtusifolia</i> (6)	9.4±1.5	28.8±1.3	9888±7334	0.45±0.31	528±227	77.7±20.3	8.6±1.7
Red figs							
<i>F. costaricana</i> (2)	0.7±0.5	11.2±1.9	9500±9758	0.04±0.02	111±58	34.7±2.3	23.0±8.5
<i>F. perforata</i> (4)	0.4±0.03	9.1±0.7	31475±13812	0.18±0.11	291±50	45.4±9.4	15.7±2.4
<i>F. colubrinii</i> (3)	0.3±0.05	8.0±0.04	12267±515	0.05±0.01	79±31	40.2±4.6	15.3±2.1

pollinators or moth or weevil infestations), both focal branch and total crop size were reestimated before final ripening.

From the first appearance of ripe fruit to the peak of ripening, the number of ripe and unripe fruits were counted on each branch daily. Fruits were considered ripe when the female fig wasps had left the fruit (visible exit holes). Persistence defines the period (days) from the first observation of the ripe fruit until the time when less than 5% of the counted fruits were left on the tagged branches. During the period of ripening, tagged focal branches were monitored twice a day: in the morning (7–9 a.m.) and in late afternoon (4–6 p.m.) for the number of unremoved fruits. Fallen fruits were counted during the morning census using fruit traps (1×1 m) that were placed under the canopy area on the ground. The fruit traps (three to ten per tree) covered between 30–70% of the canopy area. The percentage of fallen fruits was extrapolated for the entire canopy area. From each tree, 50 ripe fruits were weighed, their width and length were measured, and average fruit size was estimated.

Using binoculars during the day and night vision goggles at night, observations of frugivores visiting the fruiting trees began when the first fruits were ripe and lasted until most fruits had been removed. Diurnal sampling occurred between 6–9 a.m. and 4–6 p.m. with continuous 15-min samples taken each hour, and nocturnal sampling occurred between 6:30 and 8:00 p.m. with continuous 10-min samples taken each half hour. Whenever possible, taxa and detailed behavior of the frugivores were documented.

Calculations and statistical analysis

We estimated removal rates from the whole tree in two ways: (1) by absolute number removed per day: removal rate (fruits/day)=(crop size–fallen fruits)/persistence (days), and (2) by proportion of fruit removed per day: proportion of fruit removed=(crop size–fallen fruits)/(crop size×persistence). Both absolute removal rate and proportion of fruit removed per day are presented as the average/day for the whole persistence period. For synchrony of ripening, 20 small branches were randomly chosen and the numbers of ripe and unripe fruits were counted on each branch and the mean percent of fruit ripening on each day was calculated. Counting was conducted from the first appearance of ripe fruit to the peak of ripening. Synchrony of ripening was calculated as the average of the mean of percent fruit ripening on a given day.

We compared fruiting characteristics (e.g., fruit size and mass) among red- and green-fruited figs with Student's *t*-test. All proportions were arcsine square-root transformed prior to analysis. Stepwise regression analysis was applied to determine the relative effect of each variable (fruit mass and size, crop size, and synchrony of ripening) on removal rate and proportion of fruit removed. To assess the effect of the moon phase on fruit removal in the green-fruited *Ficus citrifolia*, we contrasted removal rates around full moon with dark nights. Based on the significant differences found, all data collected around full moon were therefore treated

separately. Results are presented as means±SD. A value of $P<0.05$ was accepted as significant. All analyses were performed using Systat 5.

Results

Comparison of fruiting characteristics in green- and red-fruited figs

Fruit size and mass across the strangler fig species ranged from species with small fruits (mean size about 8 mm, mass <1 g) to species with large fruits (mean size about 28 mm, mass >9 g) (Table 1). Crop size was large and highly variable among and within species (Table 1). Comparison of DBH and canopy area did not reveal significant differences between green- and red-fruited figs (Table 2).

However, both groups showed fundamental differences in fruit characteristics, ripening and removal pattern, and the suite of dispersers that removed them. All species of green-fruited figs produced a strong characteristic scent when ripe. Fruits of the red-ripening figs fruits ranged from pale green and whitish to pinkish during development, and turned dark red and mushy, but produced no detectable scent when ripe. Typically, crops of red-fruited figs consisted of a mosaic of differently colored fruits indicating various degrees of fruit ripening. Furthermore, the nine green-fruited fig species had significantly larger and heavier fruit, smaller crop sizes, higher synchrony of ripening, shorter persistence times, and a higher proportion of fruit removed per day (Tables 1, 2) than the three species of red-fruited figs. By comparison, the red-fruited figs produced significantly smaller and lighter fruits with lower synchrony of ripening, but had significantly larger crop sizes in terms of fruits/m² canopy area compared to green-fruited figs (average across species: 116±35 and 41±25 fruits/m², respectively), longer persistence times, and lower proportions of fruit removed per day. However, the total fruit biomass (mean crop size times fruit mass) per unit canopy area of red-fruited figs was less than a third (50±8 g/m²) that estimated for green-fruited figs (138±59 g/m²). Abortion of unpollinated fruit did not differ between crops of red-

Table 2 Comparison between green and red figs. Results are presented as means±S.D with minimum and maximum values for each measurement in parentheses. Data from observations around

full moon (three *F. citrifolia*, two *F. nymphiifolia*, one *F. dugandii*, and one *F. obtusifolia*) are excluded from this table (DBH diameter at breast height; n.s. not significant)

	Green fruits	<i>n</i>	Red fruits (<i>n</i> =9)	<i>P</i>
Fruit mass (g)	4.3±3.2 (1.33–30.65)	44	0.4±0.3 (0.22–1.1)	<0.001
Fruit size (mm)	21.6±5.7 (0.95–11.97)	44	9.1±1.3 (7.5–12.1)	<0.001
DBH (cm)	32±19 (9–82)	44	27±10 (13–47)	n.s.
Canopy area (m ²)	234±227 (31–840)	44	180±112 (53–334)	n.s.
Crop size	7,764±8,864 (260–44,100)	44	20,166±14,344 (2,600–51,600)	<0.02
Synchrony of ripening (%)	78±9 (45–96)	44	41±5 (33–54)	<0.001
Persistence (days)	6.7±2 (4–13)	37	17.2±5 (13–29)	<0.001
Removal rate (fruits/day)	993±1,144 (39–5,236)	37	1,071±820 (144–2,642)	n.s.
Proportion of fruit removed per day	0.14±0.04 (0.075–0.24)	37	0.06±0.008 (0.03–0.07)	<0.001
Proportion of fallen fruits	0.12±0.11 (0.02–0.40)	37	0.04±0.04 (0.007–0.10)	<0.001

Table 3 Patterns of bird and bat visitation for three individuals of *Ficus* species. *observation time during day. ** Each tree was observed for 10 min intervals per half hour (see methods)

	Total observation time during the day (h)*	Number of birds/ 15 min	Time spent by birds in trees (min)	Number of bird species	Estimation of bat numbers/10 min observation per half hour**					
					Tree 1		Tree 2		Tree 3	
					(0–10)	(10–50)	(>50)	(1–10)	(10–50)	(>50)
Green figs										
<i>F. citrifolia</i>	5.4±0.6	1.7±0.6	1.7±0.5	2						
<i>F. bullenei</i>	6.7±0.7	2.3±1.5	5.5±1.6	2	+			+		+
<i>F. trigonata</i>	8.8±1.2	5.3±1.6	3.1±0.6	7	+		+			+
<i>F. obtusifolia</i>	10.8±1.9	1.3±0.6	2.8±0.2	4	+			+	+	
Red figs										
<i>F. perforata</i>	16.4±2.6	17.2±3.3	3.3±0.3	28	+		+		+	
<i>F. colubrinii</i>	15.0±1.2	8.3±1.3	2.5±0.6	13	+		+		+	

Table 4 Diurnal and nocturnal removal rates of fruits and proportion of fallen fruits from green and red figs. Results are presented as means±SD. The unknown percentage is the result of missing visits. The percentage of removed fruits is related to removed fruits only after accounting for the fallen fruits. Data from observations around full moon (three *F. citrifolia*, two *F. nymphiifolia*, one *F. dugandii*, and one *F. obtusifolia*) are excluded. Values in parentheses present minimum and maximum range

	Percent of fruits removed during the day	Percent of fruits removed at night	Percent of unknown	Proportion of fallen fruits
Green fruits				
<i>F. citrifolia</i> (7)	4.9±1.8	83.1±4.9	12.1±5.8	0.09±0.08 (0.03–0.23)
<i>F. bullenei</i> (4)	9.1±5.2	80.5±12.0	10.4±5.3	0.13±0.03 (0.09–0.16)
<i>F. paraensis</i> (3)	2.1±1.8	73.8±16.0	24.1±14.5	0.06±0.02 (0.05–0.08)
<i>F. dugandii</i> (2)	23.8±7.5	60.7±12.8	15.5±14.4	0.38±0.04 (0.36–0.41)
<i>F. popenoei</i> (5)	1.3±1.7	83.7±4.6	15.0±5.2	0.10±0.08 (0.03–0.13)
<i>F. 'near trigonata'</i> (3)	6.0±5.3	84.6±6.2	9.4±4.0	0.02±0.01 (0.01–0.03)
<i>F. trigonata</i> (4)	16.1±6.6	67.6±13.1	16.3±16.4	0.23±0.09 (0.13–0.28)
<i>F. nymphiifolia</i> (3)		92.6±5.7	7.4±5.5	0.02±0.01 (0.01–0.04)
<i>F. obtusifolia</i> (5)	3.6±5.6	84.8±6.4	11.7±5.3	0.08±0.06 (0.02–0.17)
Red fruits				
<i>F. costaricana</i> (2)	74.7±7.0	15.2±3.0	9.8±2.9	0.08±0.03 (0.06–0.10)
<i>F. perforata</i> (4)	69.7±13.1	19.0±9.2	11.3±10.7	0.02±0.01 (0.07–0.03)
<i>F. colubrinii</i> (3)	60.7±23.8	16.7±2.5	22.7±21.4	0.01±0.003 (0.01–0.011)

and green-ripening species (18%, $n=4$ crops, and 16%, $n=17$ crops, respectively), and therefore does not appear to be responsible for these differences.

Observations of frugivores

The relative abundance (number of animals per 15-min observation) of birds documented at red-fruited figs was higher than at green-fruited figs (Table 3). For example, 28 species of fruit-eating birds were recorded at the red-fruited fruits of *F. perforata* (Table 3). With the exceptions of *F. dugandii* and *F. trigonata*, fruit-eating birds were rarely observed visiting and eating green-fruited figs. In contrast, fruit-eating bats were always observed in large numbers at green-fruited figs and represented their major visitors, as reflected by numerous bat feces and few bird droppings in or near these trees. Only few bats were documented at red-fruited figs. Birds and bats differed in their feeding behavior. The birds tended to stay for prolonged periods of time (>5 min) in the trees, whereas bats approached fig trees only briefly, took a

fruit, and flew with it to a temporary dining roost within 200 m of the tree (Handley and Morrison 1991; Table 3).

Occasionally, a few opossums (*Caluromys* sp.) were observed during the night at both red- and green-fruited figs (*F. citrifolia*, *F. perforata*, *F. trigonata*). Other mammals that we observed eating figs included Howler monkeys (*Alouatta palliata*) on *F. obtusifolia*, coatis (*Nasua narica*) on *F. dugandii*, *F. popenoei* and *F. perforata*, and kinkajous (*Potos flavus*) on *F. colubrinii* and *F. costaricana*.

Factors influencing absolute removal and proportion of crop removed

Both red- and green-fruited figs had very high proportions of total fruit removed, averaging 80% or more of the whole fruit crop (Table 4) with the total proportion removed slightly higher in the red-fruited species (green-fruited figs: 88±11.5%; red-fruited figs: 96±4.6%). In general, green-fruited figs were mainly removed during the night (79±9%) with the exception of *F. dugandii* and

F. trigonata that were also appreciably removed during the day (Table 4). In contrast, red-fruited figs were mainly removed during the day ($68\pm 7\%$) and to a lesser degree at night (Table 4).

Multiple regressions lumping crops across all species including crop size, fruit size, and synchronization of ripening were performed on absolute and proportional daily removal rates. These analyses showed that fruit size did not affect absolute removal rate or proportion of fruits removed per day. However, absolute removal rate

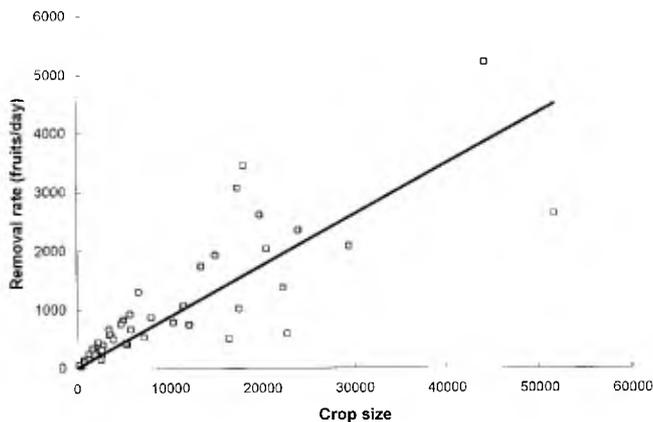


Fig. 1 Absolute removal rate per day in relation to crop size ($y=0.075x+205.30$, $r^2=0.71$, $n=46$, $F=122.5$, $P<0.001$)

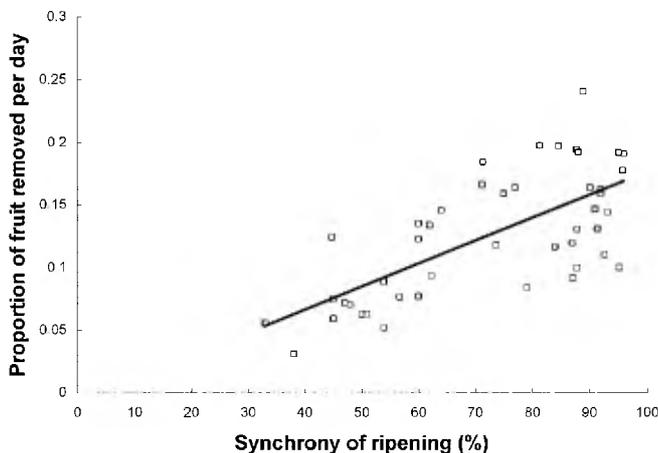


Fig. 2 Relationship between proportion of fruit removed per day and synchrony of ripening ($y=0.0018x-0.0078$, $r^2=0.48$, $n=46$, $F=39.65$, $P<0.001$)

Table 5 Comparison of nocturnal removal of *F. citrifolia* fruits on nights around new moon versus nights around full moon. Results are presented as means \pm SD (*n.s.* nonsignificant)

	Non-moon-affected trees ($n=8$)	Moon-affected trees ($n=3$)	Significance
Fruit mass (g)	1.39 \pm 0.33	1.52 \pm 0.34	<i>n.s.</i>
Fruit size (mm)	15.14 \pm 1.22	15.60 \pm 1.37	<i>n.s.</i>
Crop size	7,818 \pm 6469	11,733 \pm 9306	<i>n.s.</i>
Persistence (days)	5.60 \pm 0.53	9.30 \pm 0.57	$P<0.0011$
Removal rate (fruits/day)	1,523 \pm 1226	767 \pm 713	$P<0.05$
Proportion of fruits removed	0.16 \pm 0.04	0.07 \pm 0.03	$P<0.003$
Proportion of fallen fruits	0.09 \pm 0.08	0.37 \pm 0.06	$P<0.006$

per day was influenced by crop size (standard partial regression coefficient=0.88, $P<0.001$; Fig. 1) and to a lesser extent by synchrony of ripening (0.33, $P<0.008$, multiple $r^2=0.77$). On the other hand, the proportion of fruits removed per day was mainly influenced by synchrony of ripening (standard partial regression coefficient=0.64, $P<0.001$; Fig. 2), and to a lesser extent by crop size (0.29, $P<0.005$). Thus, across individual trees of all species, large crops had higher removal rates, implying that they attracted larger numbers of frugivores than smaller crops. With greater synchrony of ripening, larger numbers and proportions of fruit were removed over shorter periods of time.

We then tested whether the same patterns were found both between and within species. First analyses were performed on species means and the pattern was similar to the above analysis: mean absolute removal rate per day=0.080 \times crop size+132.28, $r^2=0.75$, $n=12$, $F=30.2$, $P<0.001$; and mean proportion of fruit removed per day=0.0019 \times synchrony of ripening-0.0145, $r^2=0.59$, $n=12$, $F=14.5$, $P<0.003$). The same analyses were then performed using individual crops within species and the results were again similar (Appendix 1). Thus the same pattern was observed on individual trees both within and across species, and across species means.

We further tested the possible influence of moon phase on removal rates of green-fruited figs. Some frugivorous bats are reported to exhibit lunarphobia and drastically reduce their foraging activity around full moon (Morrison 1978b). We compared removal rates of *F. citrifolia* from nights around new moon with nights around full moon (Table 5). Fruit mass, fruit size, and crop size did not differ significantly among trees. However, nocturnal removal rates and proportion of fruits removed were significantly lower in trees that produced ripe fruits during full moon. In contrast, persistence as well as the proportion of undispersed fruit increased significantly.

Estimated number of consumers of green-fruited figs

Ten of the 20 frugivorous BCNM bat species feed predominantly on figs (Kalko et al. 1996b). Adult body mass of these bats ranges from small (<10 g) to large (>70 g) and is positively correlated with the mass of the fruits they take (Bonaccorso 1979; Kalko et al. 1996b). To estimate the significance of fig fruit production for the popu-

lations of frugivores, we selected one large fruit bat (*Artibeus jamaicensis*, 50 g) feeding on *F. obtusifolia* and one small fruit bat (*A. phaeotis*, 12 g) feeding on *F. citrifolia*. Dietary studies on *A. jamaicensis* revealed that this bat eats about 94 g per night (10 fruits) of *F. obtusifolia* (E.K.V. Kalko, unpublished data). Feeding experiments with the small *A. phaeotis* revealed that this bat eats about 21 g per night (14 fruits) of *F. citrifolia* (C. Korine, unpublished data). For our estimates, we assumed that bats take all of the fruits removed at night and that individual bats feed consistently every night at the same tree throughout its fruiting period. These assumptions largely conform to previous studies on the foraging behavior of *A. jamaicensis* on BCI (Morrison 1978a).

According to our estimates, the average crop of the large-fruited *F. obtusifolia* of 528 m² crown area with a total of 84.8% of the fruits removed at night would feed roughly 97 large *A. jamaicensis* per night (834 bat-nights). The average crop of the small-fruited *F. citrifolia* with 97m² crown area and a total of 83.1% fruits removed at night would feed roughly 102 small frugivorous bats per night (571 bat-nights). Most of this feeding activity takes place on a few peak nights, less than 3 and 4 nights for *F. citrifolia* and *F. obtusifolia*, respectively.

Discussion

Fruit production and removal in Panamanian strangler figs

Our present results indicate that high proportions of the fruit (>80%) across all these fig species are removed by frugivores. For comparison, studies on *Virola sebifera* (Myristicaceae) and *Tetragastris panamensis* (Burseraceae) growing in the same forest show only 54% and 28% fruit removal, respectively (Howe 1990; Leigh 1999). Furthermore, the proportion of fig fruits removed is high regardless of whether the particular species produces small, red fruits that are dispersed primarily during the day by birds, or larger, green fruit that are dispersed primarily during the night by bats. In contrast to fairly constant proportions of total fruit removed over the duration of the crop, the proportion of fruits removed per day varied greatly among species. The differences were clearly related to the degree of ripening synchrony, which was relatively low in the red-fruited species, and higher in the green-fruit species. Both within and among species, we found a positive correlation between crop size and removal rate (fruit per day). In this respect, our data are consistent with most (Howe and DeSteven 1979; Howe and Vande Kerckhove 1979; Murray 1987; Gryj and Dominguez 1996), but not all (Bronstein and Hoffman 1987) studies.

We also found that nocturnal removal rates may vary substantially according to the moon phase. This is presumably due to an altered activity pattern of some fruit-eating bats around full moon. Previous studies have shown for *A. jamaicensis* and other bats that activity drops

considerably during bright moon nights, presumably as a consequence of higher predator pressure from mostly visually orienting predators such as owls (Morrison 1978b). In our study, we showed that the reduced activity of bats leads to a significant reduction in removal rate and proportion of fruit removed during full moons and a significant increase in persistence and abortion of ripe fruit.

Evidence for coadaptation between figs and their seed dispersers

We conclude that the notion that *Ficus* species attract a wide, nonselective range of frugivores from different taxa is an oversimplification that needs to be specified and revised for local and regional species assemblages. Furthermore, there are several lines of evidence that suggest at least some degree of broad coadaptation and specialization among fig species and their frugivores. First, there is the clear distinction between the Neotropical figs that are primarily bat or bird dispersed. Second, there are clear differences between the New and Old World figs that correspond to the sensory capabilities of the two radically different groups of frugivorous bats that disperse them. Third, within the New World bat-dispersed species, fruit size correlates with the size of bats that disperse them. Finally, there are clear correlations between the attributes of the fruit that are related to disperser guild and the other aspect of fig biology. We will discuss these points in order.

New World bird- and bat-dispersed figs

The Neotropical strangler figs appear to separate into two major groups based on distinctive fruit characteristics that correspond to the guild of dispersers that eat their fruit (Herre 1996; Kalko et al. 1996b). Even though bats and birds may overlap in their dietary choices on the genus level (here, *Ficus*), they clearly segregate at this Neotropical site on the species level. Thus, our data are consistent with findings from other sites that dietary overlap of Neotropical fruit-eating bats and birds is low (Fleming 1979; Palmeirim et al. 1989; Gorchoff et al. 1995).

Part of the observed difference in fruiting characteristics corresponds to differences in the sensory capabilities and specificities of the frugivores. Most birds depend primarily on vision, and it is presumably difficult for them to discriminate between ripe and unripe green-fruited figs without a conspicuous visual signal (see also Wheelright and Janson 1985). Typically, red-fruited figs are visited by a range of frugivorous birds, some of them specialized frugivores (i.e., manakins) and some of them opportunistic (tanagers, tyrant flycatchers, woodpeckers) (Karr 1971). The asynchronous ripening pattern in red-fruited figs studied here leads to a "steady state" availability of fruits over a longer period of time (mean of 17 days). A similar pattern (14–18 days) was found in a published study of bird-dispersed figs in Malaysia (Lam-

bert and Marshall 1991). In contrast, the fruits of green-ripening figs species span a wide range of sizes, ripen relatively synchronously, produce very distinct aromas, and are primarily consumed during the night by frugivorous bats that are relatively specialized both in degree of frugivory and on which species they concentrate (Fleming 1986). Since frugivorous bats detect ripe fruit mostly by scent (Kalko et al. 1996b), relatively synchronous ripening of many fruits within a crop ("big bang") facilitates detection of ripe fruits over long distances.

Further differences in the feeding behavior between the two groups of frugivores is likely to lead to different consequences for seed dispersal. Although both birds and bats may transit from long distances to fruiting trees, birds tend to stay and eat in the trees for longer periods of time. On any given day, a small portion of the fruit crop is consumed, with most of the seeds falling underneath the crown of the tree. In contrast, bats fly off to temporary dining roosts within about 200 m of the fruiting tree for eating (Morrison 1978b). Consequently, the association between green-fruited species and the bats is likely to result in relatively greater dispersal distances and more scattered seed shadows over a shorter period of time compared to the red-fruited species (see also Janzen 1978; Pratt and Stiles 1983; Thomas et al. 1988).

New and Old World bat dispersal of figs

The proposition that fig fruit characters exhibit broad co-adaptations with their main dispersers is further corroborated by comparisons between Neotropical and paleotropical figs and the groups of bats that disperse them. Fig fruits comprise large portions of the diet of both the Old World flying foxes (Megachiroptera) and the New World phyllostomids (Microchiroptera) (e.g., Marshall 1985; Kalko et al. 1996b). Although figs in both areas produce scent cues, fruit-eating flying foxes and phyllostomids differ in important respects in their morphology, sensory capabilities, and behavior (e.g., Fleming 1993; Kalko et al. 1996b). Flying foxes are on average much larger and rely exclusively on their vision for orientation. Phyllostomids, in contrast, are smaller and use echolocation for orientation in space, and to a limited degree for fruit detection.

Many paleotropical figs display their fruits at the tips of their mostly leafless fruiting branches that are frequently born on the trunk (cauliflorous) (e.g., Corner 1940; C. Berg, personal communication). This facilitates the access of the relatively large flying foxes. In contrast, Neotropical figs that are taken by the smaller and more maneuverable phyllostomids are usually nestled among leaves. Furthermore, paleotropical figs span a variety of colors ranging from green(ish) to red, orange, purple, and yellow with a less clear association between fruit color and size as typically found in the New World figs (Utzurum 1995; Kalko et al. 1996b). Colorful figs are likely to stand out more against the surrounding vegetation and thus are presumably easier to detect visually in dim light than the cryptic green(ish) fruit of Neotropical

figs. Thus, as is the case with the comparisons between bird- and bat-dispersed figs in the New World, differences in the fruit characteristics of Old World and New World figs correspond to the differing capabilities of the respective groups of frugivorous bats.

Fruit size and dispersal of green-fruited New World figs

Within the New World, bat species positively assort on different fig host species with respect to the relative size of the bat and the fig fruit (Kalko et al. 1996b). Recapture and radiotracking data indicate that larger species of bats travel greater distances between feeding sites and day roost, suggesting that during the course of transit flights, larger bats may disperse seeds over longer distances (Morrison 1978a; Herre 1989; Kalko et al. 1996b). Additionally, fruit size has been implicated by several other studies as a correlate of other phenomena important in the fig and wasp interaction.

Specifically, previous studies demonstrate that the size of fig fruits influences the relative importance of evaporative and diffusive cooling in full sunlight, with larger fruits requiring greater rates of transpiration in order to maintain internal temperature that will sustain the developing pollinators (Patiño et al. 1994). In general, fig species characterized by larger fruits are pollinated by more foundress wasps per fruit and produce proportionally fewer female wasps in their broods (Herre 1989). From the perspective of the fig this is important because only the female wasps disperse their pollen (Herre 1989, 1996). Furthermore, the species that are characterized by higher numbers of foundresses harbor more virulent species of host-specific nematodes (Herre 1993). In short, from the point of view of water loss, the proportion of female pollinating wasps produced, and the inefficiencies associated with increasingly virulent nematode parasites of the wasps, larger fruit would appear to present a less efficient packaging than small fruit. Therefore, we propose that the apparent disadvantages of increased fruit size might be balanced in nature by an increased capacity to disperse seeds (Herre 1989, 1996).

Figs as keystone resources in tropical forests: implications for conservation

Several observations corroborate the perceived role of figs as keystone species in tropical forests (e.g., Terborgh 1986). First, our data indicate that each small- and large-fruited strangler may feed roughly 571 small and 834 large bats, respectively, over 2–5 nights. Second, it is increasingly being recognized that fig fruits contain a range of essential nutrients and minerals, and that each fig species possesses a unique combination of minerals, proteins, lipids, and carbohydrates (O'Brien et al. 1998; Wendeln et al., in press). Together with the observation that fig fruit size and mass is positively correlated with bat size and body mass (Kalko et al. 1996b), these stud-

ies strongly suggest that a diverse assemblage of different fig species with different-size fruits is vital to support this diverse group of bats (and birds).

Third, the phenological pattern of figs means that fig fruits are available at all times of the year. Particularly in seasonal forests such as BCI, this is important because other groups of fruiting species tend to be much more seasonal, and, collectively, there are predictable seasons of fruit shortage (Foster 1982). Thus, frugivores can and do rely on the availability of fig fruits during the periods when other species are not available (Foster 1982; Milton et al. 1982; Windsor et al. 1989).

Finally, BCI is a 15-km² island in Lake Gatun, and supports a resident population of at least 3000 individuals of the common fruit bat *A. jamaicensis* (Bonaccorso 1979; Leigh and Handley 1991; Kalko et al. 1996a). In contrast, *A. jamaicensis* is rare in the Amazonian lowland forest near Manaus (E.K.V. Kalko, C.O. Handley and E.M. Sampaio, unpublished data). Although the total species diversity of figs and frugivorous bats is much higher in Manaus, the relative abundance of both fig trees and frugivorous bats that are known from other sites to primarily eat figs is much lower. Thus, along with previous studies, our data suggest that abundance and diversity of figs profoundly affect frugivore assemblages.

Moreover, an appreciation of the spatial scales over which fig pollination and frugivore dispersal occur is an essential element in designing any coherent and effective conservation program for the figs and the animals that depend on them. Although there is increasing evidence for long-range seasonal migrations in some New World fig-eating bats (E.K.V. Kalko, unpublished data), radio-tracking results and capture/recapture data of the relatively large, fig-eating *A. jamaicensis* with known roost sites in the BCNM showed average movements of 1–4 km between day roost and feeding site (Morrison 1978a; Handley et al. 1991). Transit distances appear to be smaller for smaller fig-eating species (e.g., Kalko and Handley 1994). However, recent genetic studies show that the wasps that pollinate and thereby catalyze the fruit production of any given tree in the BCNM are dependent on the composition of the fig community in surrounding areas that may exceed 100 or 200 square kilometers (Nason et al. 1998). Thus, the production of fig fruits that support Neotropical frugivore populations is dependent on the relative ecological health of areas vastly greater than that encompassing the average nightly transit distances of the frugivores.

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Appendix 1 r^2 values for the relationship between absolute removal rate and crop size within species (*n.s.* not significant)

Species	r^2	<i>P</i>
Green figs		
<i>F. citrifolia</i> (8)	0.981	0.001
<i>F. bullenei</i> (4)	0.947	0.01
<i>F. paraensis</i> (3)	0.968	<i>n.s.</i>
<i>F. dugandii</i> (2)		
<i>F. popenoei</i> (5)	0.994	0.01
<i>F. 'near trigonata'</i> (3)	0.683	<i>n.s.</i>
<i>F. trigonata</i> (4)	0.926	0.04
<i>F. nymphifolia</i> (3)	0.998	0.03
<i>F. obtusifolia</i> (5)	0.972	0.01
Red figs		
<i>F. costaricana</i> (2)		
<i>F. perforata</i> (4)	0.705	<i>n.s.</i>
<i>F. colubrinii</i> (3)	0.998	0.02

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