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Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics

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Abstract. Long-term studies of a Panamanian fig community have revealed that the figs separate into two major groups based on distinct patterns in fruit characteristics including fruit size, colour, scent and synchrony of ripening. Furthermore, these differences can be linked to sensory, morphological and behavioural capabilities of the figs' primary dispersers. One group of figs attracts primarily bats; the other group is visited mainly by birds. Whereas fruits of 'bat' figs span a wide range of size classes, ripen synchronously and remain green(ish) when ripe, all fruits of 'bird' figs have small fruit which ripen asynchronously and turn red when ripe. Among 'bat' figs,

fruit size is correlated with body size of the bats that prefer them. Based on the consistent differences between 'bat' and 'bird' fig fruits in Panama we expect similar patterns in Old World figs. Furthermore, since fig-eating bats of the Old World differ in morphology, behaviour and sensory capabilities from fig-eating bats of the New World we speculate that these differences should be reflected in differences in fruit characteristics of Old and New World 'bat' figs. Personal observations and literature reports of Old World bats and figs are consistent with our predictions.

Key words. Bats, birds, *Ficus* fruit characteristics, echolocation, foraging.

INTRODUCTION

With about 800 species, distributed worldwide in tropical and subtropical zones, *Ficus* (Moraceae) is one of the largest genera of woody plants. Furthermore, *Ficus* is the most diverse genus of woody plants with regard to habit, growth forms and life forms (Corner, 1988; Berg, 1990; Berg & Wiebes, 1992). Figs are perhaps best-known for their complex relationships with pollinating and non-pollinating wasps (for summary see Herre, this issue). Moreover, fruits of figs are important 'keystone' food resources for many frugivorous invertebrates and vertebrates, including birds, monkeys and bats (e.g. Heithaus, Fleming & Opler, 1975; Bonaccorso, 1979; Janzen, 1979; Terborgh, 1983, 1986; Beehler, 1983; Estrada *et al.*, 1984; Gautier-Hion *et al.*, 1985a,b; Handley, Gardner & Wilson, 1991c; Charles-Dominique, 1993). Generally individual figs fruit synchronized within crowns and asynchronous among individuals to maintain their pollinator wasp populations (e.g. Janzen, 1979; Milton *et al.*, 1982; Windsor *et al.*, 1989; Milton, 1991; Bronstein, 1992). Hence, a population of figs provides continuous food supply for frugivorous animals year-around (Gentry, 1974). Fig fruits become particularly important resources during seasonal bottlenecks when other

fruits are scarce (e.g. Foster, 1982; Terborgh, 1983, 1986; but see Gautier-Hion & Michaloud, 1989).

Although the importance of figs as keystone resources for many frugivores is increasingly recognized, systematic study of characteristics of fig fruits and how they relate to physiology, sensory capabilities, morphology and behaviour of the animals that eat the fruit and disperse their seeds is largely unexplored. One reason for this is the common belief that figs are generalists which attract consumers from a wide spectrum of taxa (e.g. McCure, 1966; Janzen, 1979, 1980; Leighton & Leighton, 1983). Further, most studies have focused on dispersers visiting individual fig trees rather than on local fig communities and their suites of dispersers.

We present original data on a community of figs in Panamá and focus on its relationship to local guilds of frugivores. The figs in this community show distinct patterns in fruit characteristics that can be linked to certain groups of dispersers, in particular to bats and birds. Here, we will focus on fig fruit choice in a community of New World leaf-nosed bats (Microchiroptera: Phyllostomidae). In particular we emphasize sensory, morphological and behavioural coadaptations of the bats and their association with specific fig fruit characteristics including fruit size, colour, scent and synchrony of ripening as well as dispersal distance and seed shadow. We will use the results as a basis for predicting patterns of bat–fig interactions in the phylogenetically different flying foxes (Megachiroptera) of the Old World. Based on distinct differences in feeding behaviour, sensory

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and motor capabilities and morphology between neotropical and palaeotropical fruit-eating bats we discuss how these differences should be reflected in fruit characteristics of Old World figs preferred by flying foxes. We will compare these predictions with what is known about fruit-eating bats and figs in the Old World. Finally, we will discuss syconium size of figs as an example of how trade-offs between disperser interests and pollinator interests may have shaped some of the fruit characteristics (see also Herre, this issue; Patino, Herre & Tyree, 1994).

METHODS

Database and study site

Most data originate from past and ongoing comparative field and laboratory studies on feeding behaviour and diet of neotropical bats in Panamá, including results of a 10-year study of demography and natural history of fruit-eating bats by C. O. Handley (for more details see Handley, 1991; Handley, Gardner & Wilson, 1991a). The studies, starting in 1975, have been conducted at the field station of the Smithsonian Tropical Research Institute, Barro Colorado Island (BCI). BCI (9°09'N, 79°51'W) which is situated in Gatun Lake, a part of the Panamá Canal. It is about 15.6 km² in area and covered with tropical semideciduous lowland forest. For more details see Leigh, Rand & Windsor (1982) and Foster & Brokaw (1982).

Data collection

Different fig species were censused on and nearby BCI. Ripe fig fruits were collected randomly from trees and weighed to the nearest 0.01 g on a digital balance in the laboratory. Fig fruits were considered to be ripe after the fig wasps had left (visible exit hole on the fruit), the latex content had diminished and the fruit had become soft and sweet-smelling.

To determine the role figs play in the diet of frugivorous bats we set up to ten 12 m mistnets around ripe fig trees. As the number and kind of frugivores were often highly variable from night to night and from tree to tree, we mistnetted and observed, whenever possible, at least five individual fig trees per species for several nights each. The data presented here are based on 100 capture nights with a sample size of 2567 fig-eating bats. The bats were identified, sexed, marked and weighed to the nearest 0.1 g using a Pesola spring balance. Further, we examined faeces of frugivorous bats ($N = 1721$). Fig seeds in the faeces were identified to species by differences in size, shape and surface structure based on comparisons with seeds extracted from fruits of known identity. To experimentally test fruit choice and how fruit display of fig fruits relates to the sensory cues that the bats use to detect, classify and localize ripe fruit we housed wild, untrained bats temporarily in a flight cage (about 4 m × 4 m × 2.50 m) and exposed them to real and/or manipulated fig fruits. Here, we summarize the results of the behavioural experiments (Kalko & Condon, 1993). Details, however, will be published elsewhere (Kalko, in prep.).

To describe the bats' natural feeding behaviour we observed the bats in the field with a night vision scope and

used a multiframe unit and stereophotography to photograph foraging bats. Simultaneously the echolocation signals of the bats were recorded allowing the correlation of foraging and echolocation behaviour. For more details on methods see Kalko & Schnitzler (1993). Data for flying foxes are based largely on literature and on field observations by E. K. V. Kalko in Ein Gedi, Dead Sea, Israel.

RESULTS

Fig community

We documented and identified seventeen species of figs at our study site. The figs belong to two subgenera, *Pharmacosycea* and *Urostigma* (Table 1). The four species of *Pharmacosycea* are free-standing. The species of *Urostigma* are variable in life forms. Some are frequently free-standing, but most are strangling or hemi-epiphytic (e.g. Herre, 1989). In addition to differences in growth form and leaf shape, the species of figs differ in a number of fruit characteristics including size, synchrony of ripening, and colour of the ripe fruit (Table 1; Herre, this issue).

Bat community

Of the sixty-six species of bats known to occur on BCI (Bonaccorso, 1979; Handley *et al.*, 1991a; Kalko, Handley & Handley, 1996) more than half (thirty-eight species) belong to the speciose and ecologically diverse family of leaf-nosed bats (Phyllostomidae) endemic to the tropics and subtropics of the New World (e.g. Novack, 1991; Koopman, 1993). Although it is known that some frugivorous phyllostomids (subfamily *Stenodermatinae*) occasionally include other foods in their diet, such as insects and leaves (e.g. Gardner, 1977; Willig, Camilo & Noble, 1993; Zortea & Mendes, 1993; Kunz & Ingalls, 1994), fruits, in particular figs, constitute the dominant portion of their diets (e.g. Tuttle, 1968; Heithaus *et al.*, 1975; Vazquez-Yanes *et al.*, 1975; Fleming, Heithaus & Sawyer, 1977; Gardner, 1977; Morrison, 1978; Bonaccorso, 1979; August, 1981; Bonaccorso & Gush, 1987; Handley *et al.*, 1991c). On BCI, about half of the phyllostomids (twenty species) are frugivorous of which ten species regularly feed on fig fruits (Table 2). The fig-eating bats span a wide range of size classes, ranging from very small (around 9 g) to very large (around 70 g) bats (Table 2).

Characteristics of fig fruits and their relation to dispersers

Fruiting figs, in particular the free-standing *F. insipida* with large green fruit and *F. yoponensis* with medium-sized green fruit, are visited by a variety of frugivorous vertebrates, including frugivorous birds such as toucans (*Rhamphastos* spp.), parrots (*Amazona* spp.) and guan (*Penelope purpurascens*) as well as terrestrial and arboreal mammals such as agouti (*Dasyprocta punctata*), peccary (*Pecari tajacu*), kinkajou (*Potos flavus*), coati (*Nasua narica*), opossums (*Caluromys derbianus*, *Philander opossum*), monkeys (e.g. *Alouatta palliata*, *Cebus capucinus*), and bats

TABLE 1. Fruit characteristics of figs on BCI. The characteristics refer to ripe fruit. Within the groups, the figs are arranged according to wet weight, which is given as mean \pm SD, (*n*), minimum and maximum.

	Fruit size	Wet weight (g)	Colour of ripe fruits	Synchrony of ripening	Preference by bats
Urostigma					
<i>F. colubrinii</i>	Very small	0.3 \pm 0.06 (95) 0.1–0.5	Red	Asynchronous	–
<i>F. perforata</i>	Very small	0.3 \pm 0.07 (106) 0.2–0.5	Dark red	Asynchronous	–
<i>F. costaricana</i>	Small	0.8 \pm 0.2 (100) 0.5–1.3	Red	Asynchronous	–
<i>F. pertusa</i>	Small	1.2 \pm 0.2 (137) 0.9–1.9	Green, some purplish	Synchronous	+
<i>F. paraensis</i>	Small	1.6 \pm 0.3 (162) 1.0–2.3	Green with red stripes	Synchronous	+
<i>F. citrifolia</i>	Small	1.6 \pm 0.3 (100) 1.1–3.0	Green, some purplish	Synchronous	+
<i>F. bullenei</i>	Small	1.7 \pm 0.4 (191) 0.7–2.5	Green, purplish hairs	Synchronous	+
<i>F. dugandii</i>	Small	1.8 \pm 0.3 (100) 1.3–2.4	Bright green	Synchronous	+
<i>F. 'near trigonata'</i>	Medium	3.8 \pm 0.8 (343) 1.3–6.7	Green	Synchronous	+
<i>F. popenoei</i>	Medium	4.9 \pm 0.9 (143) 3.0–7.9	Green, purplish hairs	Synchronous	+
<i>F. nympheafolia</i>	Large	8.3 \pm 1.1 (85) 5.3–10.7	Bright green	Synchronous	+
<i>F. obtusifolia</i>	Large	9.5 \pm 1.4 (95) 5.8–12.7	Dark green	Synchronous	+
<i>F. trigonata</i>	Large	10.1 \pm 1.6 (88) 6.6–14.5	Green with red dots	Synchronous	+
Pharmacosycea					
<i>F. yoponensis</i>	Medium	3.1 \pm 0.7 (100) 1.7–5.5	Green with white spots	Synchronous	+
<i>F. maxima</i>	Medium	4.9 \pm 0.8 (77) 3.2–6.6	Green, some reddish	Synchronous/ Asynchronous	+
<i>F. insipida</i>	Large	9.5 \pm 1.3 (200) 6.6–12.3	Green with white spots	Synchronous	+
<i>F. glabrata</i>	Very large	37.6 \pm 8.9 (56) 23.0–59.0	Green with white spots	Synchronous	?
<i>F. tonduzii</i>	Very large		Green with white spots	Synchronous	+

TABLE 2. Common fig-eating bats of BCI. Bats are arranged in order of mean weight per species. Weight and forearm length are given as mean \pm standard deviation. Weight is taken from adult males only.

	Size class	Weight (g)	Forearm length (mm)
<i>Vampyressa pusilla</i>	Very small	08.6 \pm 0.9 (71)	30.3 \pm 0.7 (28)
<i>Artibeus watsoni</i>	Small	12.5 \pm 1.2 (78)	38.2 \pm 1.2 (15)
<i>Artibeus phaeotis</i>	Small	13.0 \pm 1.4 (62)	39.1 \pm 1.5 (44)
<i>Vampyressa nympheaea</i>	Small	13.7 \pm 0.9 (11)	36.8 \pm 1.5 (14)
<i>Platyrrhinus helleri</i>	Small	15.8 \pm 2.0 (12)	38.8 \pm 1.0 (15)
<i>Uroderma bilobatum</i>	Medium	17.8 \pm 2.1 (142)	42.4 \pm 1.3 (131)
<i>Chiroderma villosum</i>	Medium	22.1 \pm 1.4 (44)	44.8 \pm 1.6 (29)
<i>Vampyrodes caraccioli</i>	Medium	36.4 \pm 2.8 (82)	55.3 \pm 1.1 (39)
<i>Artibeus jamaicensis</i>	Large	49.3 \pm 3.7 (616)	57.5 \pm 7.0 (292)
<i>Artibeus lituratus</i>	Very large	68.5 \pm 5.2 (169)	70.1 \pm 2.5 (216)

(e.g. Milton, 1980; Howe, 1982; Handley *et al.*, 1991c). Although many frugivorous animals eat figs, bats appear to be among the most important dispersers for this neotropical fig community. First, frugivorous bats on BCI occur in large numbers and consume large quantities of figs

year-round (Handley & Leigh, 1991; Handley *et al.*, 1991c; Kalko, 1996; Leigh & Handley, 1991). On BCI, for instance, a conservative estimate of fig consumption by bats is about 28 kg dry weight per hectare per year, compared with about 20 kg dry weight of figs per hectare per year for howler

monkeys (*Alouatta palliata*), the other major consumer of figs on BCI (e.g. Milton, 1980; Handley & Leigh, 1991). Secondly, monkeys, including howler monkeys, often eat unripe figs and crush many viable seeds while masticating, thus acting largely as seed predators. Bats, on the other hand, strongly prefer ripe figs. They ingest large numbers of viable seeds and defecate them undamaged usually while commuting between fig trees and roosts (e.g. Handley *et al.*, 1991c).

Based on our observations on the BCI fig community, we distinguish between figs mainly attracting bats and figs that are not attractive to bats but are primarily visited by birds. The two groups of figs differ in a number of fruit characteristics, in particular size, scent, colour and synchrony of ripening. Thirteen of the seventeen species of figs found on and nearby BCI are frequently visited by large numbers of frugivorous stenodermatines (Table 1). We found bite marks from medium and large-sized bats also on *F. glabrata*, which produces the largest fruits among the figs studied. However, we have no direct observations of bats actually eating and dispersing the seeds of this fig. Since *F. glabrata* grows along shores dispersal by stream currents and/or fish is likely. The thirteen species of 'bat' fig species generally produce 'big-bang' crops where the whole fruit crop, often tens of thousands of fruits, ripen synchronously within a few nights and frequently attracts hundreds of bats at night. Typically, the 'bat' fig fruits do not undergo substantial colour changes when ripening. Ripe fig fruits are usually dull-coloured, green or greenish with some white or red spots and with or without hair (Table 1). In all the thirteen species attracting bats we perceived a pleasant, fruity, species-specific scent of the fruits which became noticeable to us one or two days after the fig wasps had left the fruit and they became soft. Often, we could detect fig trees bearing ripe fruits at distances of up to several hundred metres by scent alone.

In contrast, at the other three figs (*F. colubrinii*, *F. costaricana* and *F. perforata*) we did not catch or observe large numbers of frugivorous bats. In a few instances we found faeces of small bats containing fig seeds on foliage around these figs. The faeces were verified by M. Varn as bat faeces by means of uric acid contents. Overall, however, our results indicate that these figs are not attractive to bats. Instead, they are primarily visited by small to medium-sized diurnal frugivorous birds such as tanagers (e.g. *Thraupis* spp.), flycatchers (e.g. *Myiozetetes* spp.) and orioles (e.g. *Icterus* spp.). The fruits of the 'bird' figs are very small (<1 g). *F. costaricana* produces new syconia asynchronously while in *F. perforata* and *F. colubrinii* crops are initiated synchronously. In all three species ripening of the fruit is asynchronous within a crop. Individual figs produce ripe fruits continuously over several weeks. Typically, the fruits turn red when ripening (Table 1). The ripe fruits are very soft, sticky and sugary. In contrast to the noticeable scent of 'bat' figs, we could not detect any particular scent associated with ripe fruits of 'bird' figs.

Not only are there gross differences between the fruits of 'bird' and 'bat' figs but there also are differences among the latter, particularly in size. Figs which are visited and eaten by bats on a regular basis range in size from small fruits

(mean 1–2 g) to large fruits (mean 8–10 g; Table 1). Although the density of pulp of fruits from various species differs and the fruit expand in diameter after the release of the wasps, we found that the weight of ripe fruits gives a good estimate of size and seed number (see Herre, 1989). We found a significant correlation between mean wet weight of fig fruits and mean weight of fig-eating bats caught at the respective trees ($r=0.76$, $df=9$; $P<0.01$). Large fruited figs attracted species of bats, smaller fruited figs attracted smaller species of bats (Fig. 1). Conversely, the diet of larger species of fig-eating bats was dominated by larger fruited figs and the diet of smaller species of fig-eating bats consisted almost exclusively of smaller fruited figs. A similar trend has been shown by Bonaccorso (1979) for larger fig-eating bats.

Interestingly, if we exclude the *Pharmacosycea* and the free-standing *F. dugandii* from our analysis and compare only species of the *Urostigma* group with strangling or hemi-epiphytic habits we find an almost linear correlation between mean wet weight of fruit and mean weight of bats ($r=0.98$, $df=6$, $P<0.001$). There is almost no overlap in sizes of bats consuming larger fruited and smaller fruited stranglers and hemi-epiphytes. In comparison, the smaller fruited, free-standing *F. yoponensis* (*Pharmacosycea*) as well as the free-standing *F. dugandii* (*Urostigma*) are not only visited by smaller bats but also by a rather high proportion of larger bats (Fig. 1). A detailed analysis of individual species of bats visiting specific fig trees will be published elsewhere (Kalko *et al.*, in prep.).

Fruit display and its relation to the sensory and flight capabilities of stenodermatines

To understand how fruit display of figs is related to the sensory capabilities of bats we examined cues used by stenodermatines to detect, classify and localize figs. These bats echolocate and have well developed visual and olfactory senses (e.g. Wimsatt, 1970; Hill & Smith, 1984). Further, leaf-nosed bats emit short, multiharmonic, frequency-modulated signals at high frequencies (e.g. Belwood, 1988). The physical properties of these signals are well suited to localize targets and to provide information on size, shape and texture of objects (e.g. Schnitzler & Henson, 1980; Schnitzler & Kalko, 1996; Simmons & Stein, 1980). However, the 'bat' fig fruits we studied are mostly born in leaf-axils, frequently in clusters, and interspersed by leaves, which often obscure the fruits. This makes these figs very difficult targets for echolocation, in particular when echoes from the target (fruit) are buried in clutter echoes from surrounding obstacles such as leaves and branches. Presumably, any kind of overlap may mask important information from the bats and makes classification of individual targets amidst clutter echoes extremely difficult if not impossible (e.g. Kalko & Schnitzler, 1993; Schnitzler & Kalko, 1996). Moreover, echolocation signals, in particular the short, high-frequency, low intensity signals of the stenodermatines can operate only at short-range because high frequencies are rapidly attenuated in air (e.g. Griffin, Novick & Kornfield, 1958).

New World leaf-nosed bats are known to use olfactory cues in foraging (e.g. Laska & Schmidt, 1986; Rieger & Jacob, 1988; Laska, 1990). We have exposed untrained, wild

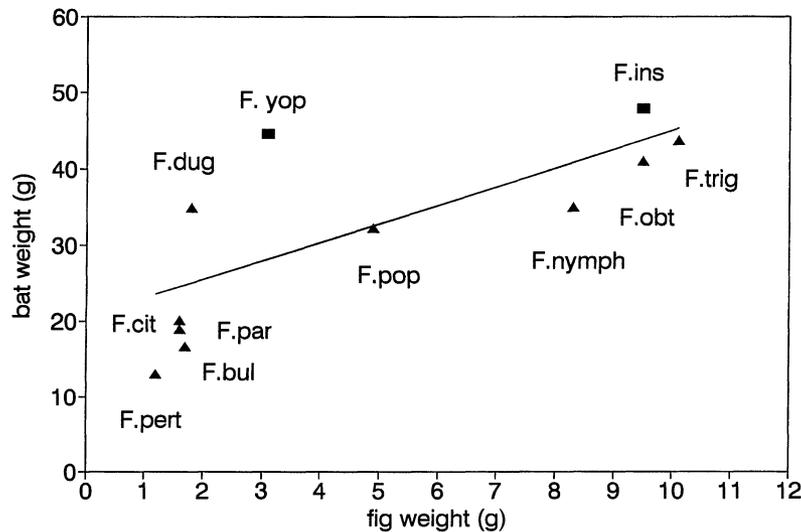


FIG. 1. Correlation of mean fig weight with mean weight of fig-eating bats caught near fig trees bearing ripe fruits. For mean fig weight see Table 1. The number of bats caught at the respective trees are given bracketed in the following list: F. bul = *F. bullenei* ($n=295$); F. cit = *F. citrifolia* ($n=128$); F. dug = *F. dugandii* ($n=212$); F. ins = *F. insipida* ($n=630$); F. nymph = *F. nymphaefolia* ($n=121$); F. obt = *F. obtusifolia* ($n=303$); F. par = *F. paraensis* ($n=73$); F. pert = *F. pertusa* ($n=51$); F. pop = *F. popenoei* ($n=236$); F. trig = *F. trigonata* ($n=100$); F. yop = *F. yoponensis* ($n=418$). ▲ = Pharmacosycea. ■ = Urostigma.

bats (*Artibeus jamaicensis*, *A. lituratus*) to ripe figs in ongoing behavioural experiments in a flight cage. We then manipulated size, shape and surface structure of the fruits and subsequently excluded visual, olfactory and echolocation cues from the bats. These experiments have shown that scent is the primary cue used by the bats to detect, classify and also to localize ripe figs (Kalko & Condon, 1993; Kalko, in prep.). The species-specific scent of ripe figs alone was sufficient to elicit search and approach behaviour and to allow discrimination among various species of figs.

However, all fig-eating bats studied continuously emitted echolocation signals in flight and while approaching ripe figs. Echolocation plays an essential role in the bat's orientation in space, in particular for avoidance of obstacles and presumably also for the localization of the branch with the fruit at close range (Kalko & Condon, 1993; Kalko, in prep.; Schnitzler & Kalko, 1996; Thies, 1993). Thus, orientation by echolocation combined with the use of scent gives phyllostomids access to ripe fruit even in total darkness.

Wing shape is another important factor in the access of stenodermatines to ripe fig fruits. These frugivores are characterized by relatively broad and moderately long wings resulting in a rather low aspect ratio. Wing shape coupled with small body size adapts them to rather slow and manoeuvrable flight (e.g. Norberg & Rayner, 1987; Fleming, 1993). Their flight capabilities in combination with echolocation allows these bats to manoeuvre around leafy branches within the canopy to get to the ripe fig fruits and to take fruit in flight.

Feeding behaviour of fig-eating stenodermatines

Field and laboratory observations and a literature survey reveal a consistent pattern of feeding behaviour in fig-eating

stenodermatines. The bats become active after dusk and fly from their day roost to a tree with ripe fruits. Approaching often from within the tree's crown the bats circle around branches bearing ripe fruits. They select a cluster of ripe fig fruits or a single fruit and make repeated approaches (usually three to four) before they attempt to take a fruit. Having pinpointed a fig fruit, the bats then bite into the fruit in flight and try to pull it off. Only rarely does a bat land for an instant on or near a ripe fig fruit. Usually, stenodermatines do not process the fruit in the fig tree itself. Instead, the bats carry the fruit in their mouth to a nearby temporary dining roost. Dining roosts of *Artibeus jamaicensis* have been located in an area up to 200 m away from the fruiting tree (Morrison, 1978; Handley & Morrison, 1991). A high risk of predation may be one of the reasons bats move away from a fruit tree as soon as they have taken a fruit (Howe, 1979). Once at dusk we observed two boas concealed among leaves of a *F. citrifolia* with ripe fruit presumably waiting for bats to arrive. On several occasions we saw spectacled owls (*Pulsatrix perspicillata*) approaching ripe fig trees and pursuing bats in flight. We frequently have caught black and white (*Ciccabor nigrolineata*) and mottled owls (*C. virgata*) in nets set for bats. Opossums (*Didelphis marsupialis*, *Philander opossum*) also are potential predators (Handley & Morrison, 1991; unpubl. observations).

In the dining roost, the bats process the fig. They manipulate the fruit with their thumb claws, bite off chunks of pulp, masticate it and squeeze out the juice by pressing the pulp with the tongue against the rigid palate. The bats then swallow the juice and spit out the residual pulp. As the bats often use a dining roost for several nights, piles of pellets accumulate on the ground. Our laboratory studies have shown that the large *Artibeus* consume five to fifteen figs per night, more than their body weight (e.g. Handley & Leigh, 1991; Morrison, 1978). However, much of the fruits' bulk is spat out as dry pellets and, as the bats urinate

and defaecate frequently, they rapidly get rid of the excess water and bulk load. While processing the fruit stenodermatines discard part of the fig seeds and ingest part of them with the fruit juice (e.g. Morrison, 1978; Humphrey & Bonaccorso, 1979; Handley & Morrison, 1991). Morrison (1980) reported that *Artibeus jamaicensis* swallowed up to 80% of the seeds of a fig. Furthermore, apparently stenodermatines swallow mostly good seeds and discard bad seeds (seeds destroyed by fig wasps) while eating (Janzen, 1978; Morrison, 1978; pers. obs.). Most seeds in the faeces of fig-eating bats are viable (e.g. Morrison, 1978). Actually, an ongoing study of seed germination in BCI figs (Handley & Garwood, in prep.) shows that seeds from bat faeces do not differ in rates of germination from seeds from ripe figs. In comparison, most of the ripe fruits that dropped to the ground rotted and their seeds did not germinate. Fig seeds profit by passage through a bat's gut since seeds separated from pulp can dry after defaecation, enhancing germination by reducing the loss to fungus.

Seed shadow

The food passage time in stenodermatines is rather short, roughly 10–45 min (Morrison, 1978, 1980; pers. obs.). Consequently, bats defaecate fig seeds during commuting flights between fruiting trees, dining roosts and day roosts. Further, capture–recapture data, radiotracking observations and analyses of faeces indicate that individual bats may visit several trees, sometimes of different species, during the course of a night (Morrison, 1978; Handley & Morrison, 1991). Thus, through their mobility and their foraging behaviour, these bats are important agents for seed dispersal and seed shadow of figs. Although most of the seed dispersal by stenodermatines is local, primarily near a fruiting tree, some is also long distance, in particular when fruiting trees are far from day roosts. The feeding behaviour of fig-eating bats contrasts with fig-eating monkeys and birds which, according to our observations, frequently eat in the tree and often stay for longer time (see also Bronstein & Hofmann, 1987). The birds usually swallow small fruits whole or drop half-eaten fruit. To reach the next tree with ripe fruits, they either hop from branch to branch or take short flights. Hence, the seed shadow created by leaf-nosed bats should be more dispersed, whereas the seed shadow generated by birds should be more concentrated directly or near the fruiting tree (e.g. Janzen, 1978; Fleming & Heithaus, 1981; Pratt & Stiles, 1983; Thomas *et al.*, 1988).

To infer potential home ranges of fig-eating stenodermatines we used capture/recapture rates of marked bats from the long-term project on demography and natural history of bats on BCI (Handley, Gardner & Wilson, 1991b) to calculate mean distances between capture and recapture sites. We found that differences in potential home ranges of fig-eating stenodermatines appear to be associated with the bats' size. Larger species tended to have larger mean distances between capture and recapture sites than smaller species.

For example, 43% of the recaptures of the very small *Vampyressa pusilla* and 84% of the recaptures of the small *Artibeus watsoni* occurred within 500 m of the original

capture site (see also Kalko & Handley, 1994). Moreover, 100% of the recaptures of *Vampyressa pusilla* and 96% of the recaptures of *Artibeus watsoni* were within 2000 m of the original capture site. For the large common fruit-bat, *Artibeus jamaicensis*, mark–recapture data as well as radiotracking studies show that these bats frequently travel 3–4 km, sometimes up to 6 km, between day roosts and netting sites in short periods of time (Morrison, 1978; Handley & Morrison, 1991). Further, studies in Jalisco, Mexico, have shown distances of up to 10 km between roost and feeding sites (Morrison, 1978).

The medium-sized *Chiroderma villosum* and *Uroderma bilobatum* as well as the very large *Artibeus lituratus* are exceptions. Although many of these bats were captured and marked during the 10-year long-term study on BCI, capture rate varied seasonally and recapture rate was extremely low (Kalko, Handley & Handley, 1996). Hence, most of these bats may only be transient visitors to BCI and may migrate with fruit availability as do some neotropical frugivorous birds (Loiselle & Blake, 1991). Consequently, since frugivorous bats are important dispersers of seeds not only of figs but of other fruits (e.g. Charles-Dominique, 1986, 1993; Foster, Arce & Wachter, 1986; Fleming, 1988) they are also important agents for conservation.

DISCUSSION

This study shows differences in fruit traits for a group of sympatric, neotropical fig species and how this relates to different dispersers. Our results strongly suggest that specific, predictable suites of fruit characters of neotropical figs are associated with dispersal by bats or birds.

Comparison of characteristics of 'bat' and 'bird' fig fruits

We found traits of fig fruits linked primarily to bat dispersal to include dull colouration of ripe fruit, largely synchronous ripening pattern of fruits within a crop and variable fruit size. On the other hand, traits of fig fruits linked primarily to bird dispersal included small fruit ripening red and asynchronous ripening of fruits within crops. These findings are supported by earlier studies (e.g. van der Pijl, 1957; Morrison, 1978; Bonaccorso, 1979; August, 1981; Utzurrum, 1984, 1995; Bronstein & Hoffmann, 1987). The observed differences between 'bat' and 'bird' fruit are not restricted to figs, but are also in accordance with general observations of fruit characteristics and their dispersers (see van der Pijl, 1957, 1982; Breitwisch, 1983; Janson, 1983; Jordano, 1983; Knight & Siegfried, 1983; Scott & Martin, 1984; Wheelright & Janson, 1985; Gautier-Hion *et al.*, 1985a; Willson, Irvine & Walsh, 1989; Willson & Whelan, 1990; Charles-Dominique, 1993).

The dull colouration of ripe 'bat' fig fruits, in combination with scent production, can now be better understood in the light of our findings that stenodermatines do not rely on visual or echolocation cues but use scent as the primary cue to detect, classify and to localize ripe fig fruits. However, echolocation also plays a crucial role in obstacle-rich environments such as the canopy of fig trees for the approach

and assessment of ripe fruit. The characteristic ripening pattern of 'bat' fig fruits with high within-crop synchrony further heightens the effect of the olfactory cues that the ripe figs produce to attract scent-orientating dispersers.

The predictable relation of certain fruit trees with suites of dispersers is well illustrated by contrasting results found in studies of the neotropical *Ficus pertusa*. In Costa Rica, Bronstein & Hoffmann (1987) found that the small (about 1 g) fruits of this species turn red when ripe, and attract mainly birds. In our study area in Panamá, however, ripe fruits of *F. pertusa* remain green(ish) when ripe, only a few turning slightly purplish. Furthermore, we detected a faint, but persistent fruity scent in the ripe figs. Here, mistnetting and observations with a night vision scope indicate that *F. pertusa* attracts mainly bats. However, it must first be determined whether the Panamanian and the Costa Rican fig may represent two species. Ongoing molecular studies will address this.

Figs and bats as a model system for testing the influence of disperser on characteristics of fruits

Assuming that some characteristics of the fruit of neotropical figs result from selective influence from consumers (e.g. bats) raises the question whether and how this assumption can be tested further. We propose that the global distribution and diversity of figs make them a good model system for comparative studies.

Leaf-nosed bats (Phyllostomidae) which are restricted to the tropics and subtropics of the New World are the only group of echolocating bats (Microchiroptera) where frugivorous habits have developed in a number of species (Stenodermatines). However, frugivorous habits have developed also in the flying foxes (Megachiroptera). Flying foxes are limited in their distribution to tropical and subtropical habitats of the Old World. As for stenodermatines, figs represent an important dietary component for many flying foxes (e.g. Jones, 1972; Wickler & Seibt, 1976; Thomas & Fenton, 1978; Marshall, 1983, 1985; Thomas, 1984; Utzurrum, 1984, 1995; Cox *et al.*, 1992; Wiles & Fujita, 1992; Rainey *et al.*, 1995). Although stenodermatines and flying foxes show some similarities in feeding habits, they have very divergent evolutionary and phylogenetic histories (e.g. Smith, 1976; Pettigrew *et al.*, 1989; Ammermann & Hillis, 1992; Fleming, 1993; but see Simmons, 1994) and almost certainly represent independent cases of the evolution of frugivorous diets. Most importantly, they show distinct differences in morphology, sensory capabilities and behaviour (e.g. Fleming, 1993). Based on our observations on New World figs and bats we will discuss how these differences between New and Old World fruit-bats should be reflected in fruit characters of the Old World figs preferred by flying foxes.

Fruit display

As we have shown fruits of the Panamanian community of 'bat' figs are rather cryptic and thus difficult to distinguish from the surrounding vegetation. The fruits are usually borne in leaf-axils or just below the leaves. They remain

green(ish) when ripe. Stenodermatines use a combination of olfactory cues and echolocation to detect, approach and assess ripe figs. Furthermore, these bats are rather small and the low aspect ratio of their wings adapt them for slow, manoeuvrable flight (Norberg & Rayner, 1987; Fleming, 1993). As we have seen, these sensory and morphological adaptations allow stenodermatines to take fruits in flight and to access fruits within the crowns. In comparison, flying foxes have well-developed visual and olfactory systems (e.g. van der Pijl, 1957, 1982; Wimsatt, 1970; Oldfield, Tidemann & Robinson, 1993) but, with the exception of a few species of *Rousettus* (Griffin *et al.*, 1958; Henson & Schnitzler, 1980; Herbert, 1985) which produces ultrasonic clicks with the tongue, they lack echolocation. Furthermore, flying foxes are on average at least two times larger than stenodermatines (e.g. Fleming, 1993). The aspect ratio of their wings is rather high, in particular in larger species, resulting in less manoeuvrability. This adapts flying foxes for long, sustained flight (Norberg & Rayner, 1987; Fleming, 1993) but makes it difficult for most megachiropteran bats to skilfully manoeuvre in narrow spaces.

Based on these sensory and morphological differences, we predict that fig fruits preferred by flying foxes should be more exposed than neotropical 'bat' fig fruits to facilitate visually guided access for Megachiroptera. Furthermore, although flying foxes may have no colour vision and thus may perceive colours only as various shades of grey, figs ripening red, orange or yellow should be attractive to Megachiroptera as they stand out against the surrounding vegetation and are thus presumably easier to detect visually in dim light than cryptic green(ish) fruit. Moreover, figs preferred by flying foxes, should produce a characteristic scent to further facilitate detection and classification.

Although we know very little about the associations between Megachiropteran bats and figs, a number of general observations on characteristics of Old World figs appear to support our predictions. Many palaeotropical figs are known to produce their fruits at the outer tips of their branches and at specialized fruit branches on trunks. Some species of figs may even drop their leaves when the figs ripen (Compton, pers. comm.). In contrast, only a few neotropical species are deciduous and produce fruit during the leafless time. Further, the diversity in colour and size in palaeotropical figs is much higher than in the Neotropics (C. C. Berg, pers. comm.). Many figs bear rather large fruits which ripen red, orange or yellow. Fruits of neotropical figs are often smaller, they remain greenish or turn slightly yellow. Some small fruits become more or less white, sometimes with reddish stripes or turn red(dish) or orange (Berg, 1990; C. C. Berg, pers. comm.). Moreover, many palaeotropical figs produce cauliflorous fruits, which often grow in clusters. Except for a few species, cauliflorous habits are absent among neotropical figs. These fruit characteristics of palaeotropical figs may foster dispersal by flying foxes (see also van der Pijl, 1957, 1982) since colourful, rather large and exposed fruits are easier to locate visually and by scent, and they are more accessible to flying foxes than dull coloured fruits on branches inside the vegetation would be. Anecdotal observations of flying foxes visiting fig trees support this assumption (S. G. Compton, P. Michaloud &

Weiblen, pers. comm.; Uzzurum, 1995). *Ficus sycomorus*, an Old World fig, produces fruits on older wood on leafless branchlets, which may then be heavily visited by the flying fox *Rousettus aegyptiacus* (personal observations in Israel). The fruits turn red when ripe. The bats frequently approach the leafless branchlets from below, land on them and crawl along to get to ripe fruits. The branchlets are arranged on the main branches of the fig so that they point towards the open space inside the crown.

Seed shadow

As in stenodermatines, flying foxes defaecate viable fig seeds (e.g. Uzzurum & Heidemen, 1991; Izhaki, Korine & Arad, 1995; Uzzurum, 1995). Behavioural differences between flying foxes and stenodermatines should also influence size and shape of the seed shadow. Since flying foxes often forage and stay in individual trees for a prolonged time (e.g. Thomas & Fenton, 1978; Elmquist *et al.*, 1992; Uzzurum, 1995), a large part of the seed shadows created by Megachiropteran bats should be concentrated around the tree. In contrast, the main part of the seed shadows created by stenodermatines should be further away from a fruiting tree, since these bats fly with fruits to dining roosts. However, since flying foxes often have very large home ranges compared with stenodermatines, maximum dispersal distances should be higher for Megachiroptera. Anecdotal evidence supports these assumptions (e.g. Janzen, 1978; Fleming & Heithaus, 1981; Uzzurum, 1984, 1995; Thomas *et al.*, 1988). Many flying foxes commute nightly from roost sites on islands to adjacent islands or the mainland, sometimes more than 40 km each way (e.g. Cox *et al.*, 1992). A very good example of long-range dispersal of seeds by flying foxes is the recolonization of the volcanic island of Krakatau in Indonesia. Here, flying foxes were among the first vertebrates dispersing fig seeds on the island (van der Pijl, 1957; Whittaker & Jones, 1994).

Fruit size

Due to differences in foraging behaviour and body size of stenodermatines and flying foxes, fig fruit size taken by these two groups should differ. In stenodermatines, there is a strong association between fig fruit size and bat size, with larger bats taking mostly larger fruits and smaller bats taking mostly smaller fruits. Several factors appear to constrain New World fig bats in choice of fruit size. First, stenodermatines, which are rather small (the largest species, *Artibeus lituratus*, weighs around 70 g) are constrained by foraging behaviour. Since stenodermatines usually take fruits in flight and transport them to a dining roost they are limited in carrying capacity. *Ficus glabrata*, for instance, which is the largest fig near our study area, weighing around 35 g, seems to be too heavy for any of the stenodermatines to transport. Although we found bite marks on fruits collected in the field, studies in the flight cage with *Artibeus lituratus* showed that this bat was unable to carry the fruit. It is unlikely that bats process such fruits on the forest floor or in the tree itself on any large scale as they may be too vulnerable to predators in such situations (e.g. Howe, 1979).

Secondly, handling constraints, in particular gape width, are also likely to be limiting factors for fruit size, as bats take a fruit, hold onto it with their teeth and fly with it to the dining roost. Thirdly, energetic constraints due to the high costs of flight are also likely to limit the range of fruit sizes taken, particularly by larger bats. Assuming that the caloric value of figs is approximately proportional to their size, larger figs should have a higher caloric value per fruit than smaller figs. Then, considering the energy a stenodermatine has to expend to get a single fig including multiple approaches to each fruit and commuting flights between fruit tree and dining roost, it becomes obvious that smaller figs are not profitable to larger bats in order to achieve a positive net energy balance (see Morrison, 1978).

Flying foxes, on the other hand, often exhibit a rather sedentary feeding mode. They stay in feeding trees longer, eat there and reach ripe fruits by crawling up and down the branches (e.g. Jones, 1972; Uzzurum, 1984, 1995; Cox *et al.*, 1992; pers. obs.) thus reducing the high costs of commuting flights between fruiting trees and dining roost. Hence, we predict for flying foxes, in particular for larger species, that the size range of fig fruits taken by them should be much more variable than in stenodermatines. That is, larger flying foxes should also be able to include small figs in their diet, and smaller flying foxes could also feed on larger figs if they stay in the tree. In essence, we expect a large overlap in fig fruit diet among different-sized flying foxes. Moreover, considering the sedentary feeding mode of flying foxes and their larger size compared with stenodermatines, the maximum size preferred figs should be larger in the paleotropics than in the neotropics. Among flying foxes, the exceptions would be smaller species foraging in a style similar to stenodermatines, that is, taking fruits to nearby dining roosts. Here, we would expect a correlation between fruit size and bat size.

Several observations support these predictions. In general, diversity in size, colour and display of figs is much greater in the Old World than in the New World. In general, large fruits are more common in the Old World and the largest fig fruits are also found there (Corner, 1988; Berg, 1990; Mack, 1993). Figs in Africa, for instance, reach diameters up to 5–10 cm. In comparison, fig fruits in the neotropics are mostly relatively small, rarely exceeding 2–2.5 cm in diameter. Only a few species of *Pharmacosycea* produce fig fruits 4 cm or more in diameter which corresponds to weights of about 8–10 g (C. C. Berg, pers. comm.; for more see Corner, 1988; Berg, 1990; Berg & Wiebes, 1992).

In the Old World there has been only one study relating fig fruit characteristics to dispersal by bats and birds (Uzzurum, 1984, 1995). At least eleven of thirty species of *Ficus* recorded in the study area were eaten by eight species of flying foxes (Megachiroptera). The flying foxes ranged in size from 75–290 mm forearm length and were thus much larger than the bats in the Panamanian bat community (Table 2). Uzzurum (1995) found no size relationship between bat size and fig fruit size. For example, large flying foxes fed on small as well as on large fig fruits. Conversely, small- to medium-sized flying foxes were not restricted to smaller fruits but also included large fig fruits in their diet. This contrasts sharply with our observations on

stenodermatines where we found a strong correlation between bat size and fruit size. Larger bats were restricted to larger fruits and smaller bats to smaller fruits. This supports our prediction that the correlation of fruit size and bat size in flying foxes should not be as binding as it is in stenodermatines.

The differences in fruit characteristics between figs of the New and Old Worlds and the dichotomy of 'bat' fig fruits and 'bird' fig fruits in our study area in the neotropics suggest capacity for flexible evolutionary change in fruit characters at several time scales. So far, our examples have concerned only the impact dispersers may have on fruit characteristics. However, it is also important to consider other interactions which may influence fruit traits. Few, if any, characteristics function and evolve in isolation from others (Herre, this issue). For instance, differences in fruit size in neotropical *Urostigma* are related not only to differences in size of dispersers but are influenced also by the fig's interaction with pollinating fig wasps (e.g. Herre, 1989, this issue; Patiño *et al.*, 1994).

Figs are often exposed to full sunlight, which might raise the temperature inside the fruit to such a level that the fig wasps may die. Thus, figs need to cool the internal temperature of their developing fruits to keep the fig wasps alive. The relative importance of evaporative and diffusive cooling of fruit in full sunlight changes with increasing fruit size, 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 comparison, due to their small size, the red, primarily bird-dispersed figs do not require evaporation to avoid overheating. This may also explain the lack of a porous fruit surface. Additionally, fruit size has been implicated as a correlate of other phenomena important in the fig and wasp interaction. In general, figs characterized by larger fruits are pollinated by more foundress wasps per fruit (Herre, 1989). Further, species that are characterized by higher numbers of foundresses harbour more virulent species of host-specific nematodes (Herre, 1993). From the point of view of water lost, the proportion of female pollinating wasps produced and the inefficiencies associated with increasingly virulent nematode parasites of the wasp, larger fruit would appear to be a less efficient seed package than small fruit. However, as we have shown, larger fruited figs, which tend to be relatively seed-rich, are dispersed preferentially by larger species of bats, generally capable of dispersing seeds for greater distances. Therefore, it appears that the apparent disadvantages of increased fruit size are balanced in nature by an increased capacity for seed dispersal, particularly in the New World species which have been best studied.

Considering fruit choice in bats, a number of other factors also come into play. In particular, nutritional quality of fruits (e.g. amount of proteins, lipids, carbohydrates and minerals per fruit) as a basis of fruit choice has been largely neglected in studies of bat-plant interactions. Ongoing studies of the fig fruits in our study area seem to contradict the current regard of neotropical fig fruits as 'cheap' fruit containing mostly carbohydrates (see Hladik *et al.*, 1971; Milton & Dintzis, 1981; Jordano, 1983; Herbst, 1986).

Pronounced differences in nutritional quality among various species have become apparent (Kalko *et al.*, in prep.; Wendeln, in prep.). In comparison 'bird' fig fruits appear to contain very little protein. Among 'bat' fig fruits we found that ripe fruit of *Urostigma* seem to contain more carbohydrates but less protein than *Pharmacosycea* fig fruits. These differences in nutrients may be one of the underlying reasons for the observed divergence in the extent of the correlation between bat size and fig size. Studies are under way relating fig fruit choice in individual bat species to fig fruit quality (Kalko *et al.*, in prep.).

CONCLUSION AND FUTURE DIRECTIONS

In this study we present recently collected data, reanalysis of data from a long-term project and combine it with information in literature. Our studies suggest how suites of fig fruit characteristics may have evolved under consumer pressure, largely reflecting morphological behavioural and sensory capabilities of the major groups of dispersers.

We must emphasize that the predictions we have made on fruit characteristics in New versus Old World figs, based on behavioural, morphological and sensory differences in fig-eating bats need to be substantiated in greater detail. In particular, the extent of the impact flying foxes have on fig dispersal in the Old World is almost unknown. It may be that the association of flying foxes with figs is less specific than the association of stenodermatines (see Fleming, 1993; Rainey *et al.*, 1995). Furthermore, as the fruit characteristics potentially involved in fruit choice by flying foxes such as fruit colour and the presumed disregard for fruit size by larger flying foxes might lead to substantial overlap with figs preferred by birds or other groups of dispersers. Gautier-Hion & Michaloud (1989) observed in Africa that birds and the hammerhead bat, *Hypsignathus monstrosus* used similar figs for food. However, whereas birds visited the fig trees opportunistically and rather infrequently, the hammerhead bat fed regularly in these trees.

Overall, we want to emphasize the importance of augmenting detailed, individual case studies with systematic studies of larger species assemblages and communities (see Charles-Dominique, 1993; Kalko, in press). Comparative studies of communities hold the promise of revealing recurrent patterns, which otherwise may go undetected. Moreover, if we are to understand factors shaping fruit traits, the present study demonstrates quite clearly that it is not sufficient to look only at the disperser's side. For instance, in the case of figs, limitations in fruit size can only be fully appreciated when we also take into account constraints imposed by the reproductive biology of figs. However, as this symposium volume demonstrates, the concept of multifaceted approaches and comparative studies is increasingly appreciated, and we can look confidently forward for the many insights future studies will yield.

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