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SHORT COMMUNICATION

Preferences of fig wasps and fruit bats for figs of functionally dioecious *Ficus pungens*

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Figs (*Ficus* species) are an important resource for a diverse array of organisms in most tropical forests (Janzen 1979 but see Gautier-Hion & Michaloud 1989). The inflorescence of *Ficus*, hereafter referred to as the 'fig', is an enclosed receptacle lined with unisexual flowers. The flowers of *Ficus* species are pollinated by wasps that feed on galled fig ovules as larvae and that lay eggs in fig flowers as adults (Weiblen 2002). Ripe figs are consumed by vertebrate frugivores, which are the primary dispersers of fig seeds (Shanahan *et al.* 2001). The interaction between figs, pollinators and frugivores introduces the potential for conflict between the roles of raising fig wasps and dispersing seeds. Specifically, the pollination mutualism could be compromised if frugivores consumed figs containing pollinator larvae. This conflict is resolved in very different ways according to the breeding system of the fig.

Monoecy, the condition of having staminate and carpellate flowers in the same fig, is ancestral in *Ficus* (Weiblen 2000). Monoecious species produce seeds (female function) and pollen (male function) in the same fig. Pollen-laden female fig wasps are attracted to figs when the carpellate flowers are receptive, and gain access to the fig cavity through a tiny opening, or ostiole. Pollination is always associated with females attempting to lay eggs by piercing the stigmatic surface with their ovipositors. Galled flowers nourish pollinator offspring and undisturbed flowers produce viable seeds. Adult male wasps emerge to mate with females, who collect pollen from staminate flowers and leave in search of receptive figs, beginning the life cycle again. Monoecious figs become attractive to frugivores only after the pollen-bearing wasps have exited (Janzen 1979), minimizing conflicts between pollinators and frugivores.

More than half of all fig species are functionally dioecious, with male and female functions relegated to separate plants, called gall and seed figs (Kjellberg *et al.* 1987, Patel & McKey 1998, Patel *et al.* 1995). Female wasps pollinate flowers of both types but successfully oviposit only in gall figs. Carpellate flowers in gall figs nourish pollinator larvae and staminate flowers donate pollen to the emerging female wasps. Gall figs are functionally male because they produce pollen and rear its vectors. Seed figs are functionally female because wasp larvae have no opportunity to consume the seeds. In contrast to monoecy, the separate utilization of dioecious figs by pollinators and frugivores has received little attention. Patel & McKey (1998) predicted that gall figs and seed figs would differ in characteristics relevant to dispersers, but no study has tested this prediction. Lambert (1992) found frugivorous birds visiting seed figs more frequently than gall figs and fruit bats are known to feed on dioecious figs (Phua & Corlett 1989, Utzurrum & Heideman 1991).

We documented rates of pollinator visitation for a dioecious fig species in New Guinea and investigated morphology and nutritive content as potential factors governing fruit choice by fruit bats. These observations led us to develop the hypothesis that sexual dimorphism in dioecious figs is reinforced by opposing selective pressures imposed by pollinators and seed dispersers. While numerous hypotheses for sexual specialization in dioecious figs have been proposed (Harrison & Yamamura 2003, Patel & McKey 1998), this paper is the first to develop the idea of opposing selection. We argue that

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fig wasps could select for similarity during the receptive phase of fig development while fruit bats could select for dissimilarity during the dispersal phase.

Ficus pungens Roxb. is a pioneer species occurring in secondary forest and along watercourses throughout New Guinea. Trees of reproductive age produce crops continually and there is within-tree synchrony in both sexes such that figs on a given tree tend to be in the same developmental phase. Hundreds or thousands of figs per branch are visible and accessible to several resident species of fruit bat (Chiroptera: Pteropodidae). Bats are the most abundant mammalian frugivores in our study area and are reliable and effective seed dispersers (Shilton *et al.* 1999, Utzurrum 1995).

To evaluate pollinator visitation rates to gall figs and seed figs, female *Ceratosolen nanus* wasps were trapped at trees near the villages of Baitabag (145°147′E, 5°08′S) and Ohu (145°141′E, 5°114′S). Traps were set prior to the pollination phase at five trees of either sex using vertically oriented plastic dishes (18.2 cm^2, two per tree) lined with sticky Tanglefoot$^{\mathrm{TM}}$. Traps were removed after fruit development was evident, 2–8 wk later.

Physical characteristics of receptive and ripe figs were evaluated including diameter (to 0.1 mm), mass (to 0.1 g), hardness (puncture resistance), colour and odour. Gall figs were considered ripe if they ruptured with a gentle squeeze, corresponding to the period just before and during the emergence of the wasps.

To evaluate fruit choice by bats, adult individuals of *Nyctimene albiventer* (N = 2), *Paranyctimene raptor* (N = 2) and *Syconycteris australis* (N = 2) were captured in mist nets near Baitabag village. Each species consumes figs, although *Syconycteris* is less reliant on figs than the other two (Bonaccorso 1998, Dumont 2003). On the night of capture, animals were transferred to individual cages (45 cm on each side) and provided unlimited access to both wild and cultivated fruit. Over the next two evenings, individual animals were simultaneously presented with pairs of freshly picked, equally ripe seed and gall figs positioned at equal distances from the bat. Preference experiments for each animal consisted of 10 paired choices.

Ripe figs were collected from five trees of each sex. Approximately equal numbers of figs were pooled by sex for nutritional analysis owing to the large number of dried figs required for chemical analyses. Each dried sample with seeds removed included approximately 600 figs and weighed 10 g.

Crude fat, crude protein and fibre (NDF) content of the dried fig samples were ascertained using AOAC techniques (Jones 1984). Crude fat was determined through petroleum-ether extraction. Kjeldahl nitrogen was determined by digesting samples in sulphuric acid using a Cu catalyst followed by steam distillation. Nitrogen was converted back to crude protein by taking N × 6.25. NDF was calculated by boiling samples in neutral detergent and rinsing the solubles to quantify leftovers as total cell wall constituents (hemicellulose, cellulose, lignins). Soluble carbohydrate was calculated using water extraction and phenol reduction with a colorimetric assay via spectrophotometry (Strickland & Parsons 1972) with sucrose as a standard.

For the analysis of minerals, small (0.5 g) samples of dried fig were placed into Teflon PFA vials (Savillex Co.) and digested with 5 ml of concentrated nitric acid at 90 °C for about 12 h. The samples were cooled to room temperature and the volumes adjusted to 25 ml with water. Following centrifugation the clear supernatants were analysed by inductively coupled plasma atomic emission spectrometry (ICP-AES) with a power input of 1.175 kW. To ensure accuracy of the results, a control swine-feed sample (9932-AAFCO) with certified mineral values from a check programme of Association of American Feed Control Officials (AAFCO) was analysed first. Concentrations of Ca were determined for each sample by ICP-AES (GBC Integra XM2) with argon gas as a carrier. The wavelength (nm) of the emission peak for Ca was 612.222.

With respect to pollinator visitation, our results agree with those of other studies indicating that pollinators visit both seed and gall figs (Patel *et al.* 1995, Weiblen *et al.* 2001). Different numbers of pollinators trapped at gall figs (mean ± SD; 38.6 ± 18.4 pollinators per tree) vs. seed figs (22.8 ± 3.4) suggests that wasps prefer gall figs, but this difference was not significant (t = 1.77, P = 0.11, n = 5, two-tailed test). Receptive seed and gall figs also appeared indistinguishable to the investigators in size, shape and colour. For example, the mean diameter of receptive gall figs (3.11 ± 0.18 mm) and seed figs (3.14 ± 0.12 mm) was not different (t = 0.44, P = 0.66, n = 10).

During choice experiments, bats investigated ripe seed and gall figs using sight and smell. Bats bit gall figs prior to rejecting them in two instances. In all 60 choice experiments, bats consumed only seed figs. All gall figs were rejected. Although the two types were of the same texture, seed figs were brighter in colour, more strongly scented and slightly larger in diameter and mass than were gall figs (Table 1). Chemical analysis showed that seed figs contained higher proportions of soluble carbohydrates (sugar) and lipid, while gall figs contained more crude protein and dietary fibre (Table 2). Gall figs contained higher concentrations of calcium than did seed figs. Moreover, the ratio of calcium to phosphorus, an estimate of calcium availability (O'Brien *et al.* 1998), was higher in gall figs than in seed figs.

Odour and colour influence fruit choice by bats that consume neotropical monoecious figs (Kalko *et al.* 1996, Korine *et al.* 2000) and similar cues advertise ripe seed figs of *F. pungens*. While the wasp life cycle is linked to gall figs, differences in colour, odour and nutritional content

Table 1. Physical characteristics of ripe figs in *Ficus pungens* (mean ± SE).

	Diameter (mm) n = 10	Mass (g) n = 10	Hardness[‡] (g per mm^2) n = 60	Colour	Odour
Gall figs	6.6 ± 0.41	0.2 ± 0.04	146 ± 58.1	brown	absent
Seed figs	7.1 ± 0.31	0.3 ± 0.05	146 ± 38.8	bright red	pungent
P value	< 0.01*	< 0.01[†]	not significant[†]		

* t-test; [†] Mann–Whitney rank sum test; [‡] puncture resistance.

are associated with bats' overwhelming preference for ripe seed figs over gall figs. Bandicoots and birds also visit *F. pungens* (Basset *et al.* 1997), which may be attracted to the bright red coloration not usually associated with bat-dispersed figs. Nutritional analysis showed that the bats we examined prefer sweet figs (Table 2). This agrees with a recent study demonstrating that soluble carbohydrates are a fundamental source of energy for fruit bats (Dierenfeld & Seyjaget 2000). The relative indigestibility of lipids by fruit bats suggests that the higher lipid content of seed figs is not a factor guiding their selection.

Protein and mineral content have emerged as important factors mediating dietary selectivity by bats and other frugivores (Barclay 1995, Kunz & Diaz 1995, O'Brien *et al.* 1998, Thomas 1984, Wendeln *et al.* 2000). However, increased levels of these nutrients in gall figs do not induce bats to select them over seed figs. This agrees with reports that fruit bats have relatively low protein requirements (Delorme & Thomas 1999, Dierenfeld & Seyjaget 2000, Korine *et al.* 1996). Although seed figs contain less calcium than gall figs, levels are within the range for monoecious figs (O'Brien *et al.* 1998, Wendeln *et al.* 2000).

The potential benefits of higher concentrations of calcium and protein within gall figs may be outweighed by costs associated with their high fibre content. Bats chew figs in order to extract nutrients and water, producing a fibre bolus that is spat out rather than swallowed (Bonaccorso & Gush 1987, Dumont 2003). Selecting fruits with relatively low fibre and high sugar may be more efficient than devoting energy to masticating fibrous fruits containing more protein but less available sugar.

The nutritional composition of *F. pungens* differs from that of monoecious figs in several respects. While the percentage of soluble carbohydrates in seed figs exceeds values reported for monoecious figs from Panama (Wendeln *et al.* 2000), the percentages of crude fat, crude protein and fibre are within the reported ranges for monoecious species. Crude protein values for gall figs of *F. pungens* also fall in this range. Gall figs contain more calcium than all other figs, a higher per cent fibre than neotropical monoecious figs and lower percentages of sugars and crude fat (Nelson *et al.* 2000, O'Brien *et al.* 1998, Silver *et al.* 2000, Wendeln *et al.* 2000).

Our comparison of pollinator visitation rates showed that wasps visit both gall and seed figs when they are receptive and externally similar. These findings are consistent with studies documenting similarity in volatile chemical attractants in gall and seed figs (Grison-Pige *et al.* 2001). Because wasp offspring do not survive in seed figs, it would be advantageous for pollinators to avoid them (Kjellberg *et al.* 1987). However, to do so would threaten the stability of the mutualism. The similarity of the two fig types at the receptive phase has been attributed to two sources, direct selection favouring seed figs that mimic gall figs, and 'vicarious selection', the increased plant fitness associated with offspring of visitors to gall figs that are unable to avoid seed figs (Grafen & Godfray 1991).

In contrast to similarity at the pollination phase, significant differences in size, colour, odour, palatability and nutritional content emerge between gall and seed figs during the dispersal phase. Differences in fleshiness and sugar content agree with the predictions of Patel & McKey (1998), who found patterns of sexual specialization in fig phenology. We found traits that are energetically important to bats associated with the choice of seed figs, while unattractive traits like fibre are higher in gall figs.

Similarity between gall and seed figs at the pollination phase and dissimilarity between them at the dispersal

Table 2. Nutritional characteristics of ripe gall and seed figs in *Ficus pungens*.

	Soluble carbohydrates (%)*	Crude fat (%)*	Crude protein (%)*	Fibre (NDF) (%)*[†]	Ca (ppm)	Ca:P ratio
Gall figs	5.2	3.9	7.0	55.0	27 100	17.8
Seed figs	38.6	10.2	4.3	23.5	12 359[‡]	8.7

* Calculated as per cent dry weight; [†] Neutral detergent fibre, a measure of indigestible fibre; [‡] Midpoint of range.

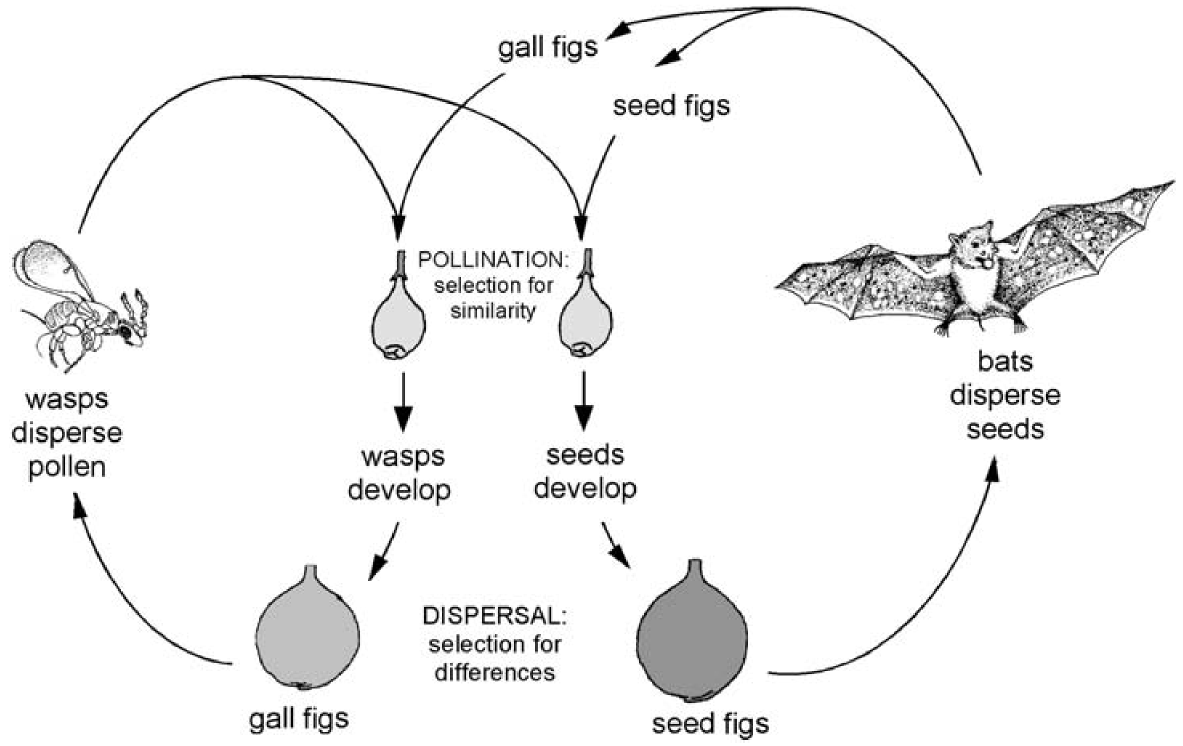

Figure 1. The life history of functionally dioecious *Ficus pungens* Roxb. All figs are pollinated by *Ceratosolen nanus* Wiebes females as they attempt to lay eggs in fig flowers. Wasps successfully lay their eggs in gall figs but not in seed figs. The two types are externally indistinguishable at the time of pollination. Selection favours similarity between seed and gall figs to ensure pollination of seed figs. Later in the life cycle, pollen is vectored by a new generation of pollinators reared in gall figs. Bats consume only ripe seed figs and disperse their seeds. At this stage, selection favours differences between seed and gall figs that focus dispersers on seed figs and discourage the destruction of the pollen vector in gall figs.

phase could reflect opposing selection by wasp pollinators and bat dispersers at different stages of fig reproduction (Figure 1). Seed figs that mimic gall figs at the pollination phase increase the female component of plant fitness through the pollination of flowers by unlucky wasps. On the other hand, dissimilarity at the dispersal phase is advantageous in both components of plant fitness. There is an obvious advantage to seed fig attractiveness to frugivores. At the same time, there could be a male fitness cost associated with the consumption of gall figs if the pollen vector has not exited. Traits discouraging consumption of gall figs by frugivores would avoid such a reduction in male fitness. While bats do not avoid gall figs completely (Phua & Corlett 1989), large accumulations of gall figs on the ground beneath parent trees relative to seed figs suggests that removal rates are substantially lower than those of seed figs (Lambert & Marshall 1991).

Another potential advantage of unattractive gall figs when resources are limiting is that nutrients in empty figs fallen to the ground could be recovered by their parent trees (Harrison & Yamamura 2003). An alternative explanation for the dramatic difference in sugar content between gall figs and seed figs is that these resources are withdrawn from gall figs to recycle them. Because gall figs are never as sweet as ripe seed figs, we believe that selection by sugar-demanding frugivores is the simplest explanation for the dissimilarity between the two sexes.

Our observations and those of other studies (Lambert 1992, Lambert & Marshall 1991, Patel *et al.* 1995, Weiblen *et al.* 1995, 2001) are consistent with the hypothesis that fig traits are subject to conflicting selection pressures imposed by pollinators and seed dispersers. We predict that further comparative studies of pollinator visitation rates and differences between ripe seed figs and gall figs will establish the generality of these findings for dioecious figs as a whole.

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