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Fig Dimorphism in Bird-Dispersed Gynodioecious *Ficus*

In Malaysian lowland rain forests, at least 29 species of *Ficus* have bird-dispersed figs (Lambert 1989). Eight of these species belong to the subgenus *Ficus*, and are gynodioecious. Plants of these gynodioecious species produce either gall figs or seed figs. Gall figs contain both male and female florets, but effectively become males because the female florets have relatively short styles and are predated by the larvae of agaonid wasps, which are the species-specific pollinators of *Ficus*. In contrast, the styles of seed figs are longer, so that incoming agaonids pollinate the florets but cannot oviposit eggs in them. Seed figs therefore produce seeds, but are not a source of pollen-carrying agaonids (Janzen 1980, Verkerke 1989).

Hill (1967), working mainly in Hong Kong, stated that there were no external morphological differences between gall and female plants except for differences in the shape and size of the figs, and sometimes in their color and seasonal occurrence. In southeast Asia, these differences have not been previously documented.

A comparison of the figs from three gynodioecious bird-dispersed strangling *Ficus* species [*F. heteropleura* Bl., *F. obscura* Bl. (var. *borneensis* Miq.) Corner, and *F. parietalis* Bl.] at Kuala Lompat, West Malaysia (3°43'N, 102°17'E, 50–80 m altitude) showed that there were distinctive, consistent differences in color, texture, and morphology between figs on male and female plants.

Gall figs were always paler in coloration than their respective seed figs, and did not exhibit the striking color changes associated with the ripening of the latter. Thus the gall figs of *F. obscura* were whitish, becoming blotchy brown before dropping, in contrast to the bright orange seed figs which ripened dark red to purple. The gall figs of *F. heteropleura* and *F. parietalis* were pale orange at all stages, while both species produced orange seed figs which ripened dark red. The texture of gall figs was rubbery at the stage before falling, but never developed the characteristic soft, fleshy nature of bird-dispersed seed figs. Ostioles of the gall figs of *F. parietalis* were notably large and appeared to open just before the gall figs fell to the ground. The broad, open ostioles of *F. parietalis* presumably assist the escape of pollen-laden female agaonid wasps. In contrast, seed figs of *F. parietalis* did not have distinctive, open ostioles at any stage of ripeness.

TABLE 1. *Comparison of mean sizes (mm) of seed figs and gall figs of two gynodioecious* Ficus *species. The value of* t, *number of degrees of freedom (df) and probability levels* (P) *are also shown.*

	Seed fig	Gall fig	*t*	*P*
F. obscura width	8.69 ± 0.60 ($N = 18$)	9.25 ± 0.64 ($N = 18$)	−8.78 (29 df)	>0.001
F. obscura length	8.03 ± 0.55 ($N = 14$)	9.50 ± 0.39 ($N = 14$)	−2.50 (27 df)	0.019
F. parietalis width	16.57 ± 1.27 ($N = 14$)	29.09 ± 1.70 ($N = 13$)	−22.71 (27 df)	>0.001
F. parietalis length	15.57 ± 1.38 ($N = 16$)	23.87 ± 2.10 ($N = 16$)	−12.79 (26 df)	>0.001

At Kuala Lompat, gall figs were always larger than the seed figs of female conspecifics. Samples of figs of *F. obscura* and *F. parietalis* were measured and *t*-tests revealed that gall figs were significantly longer and significantly wider than seed figs for both species (Table 1).

"Male" trees of *F. parietalis* and *F. obscura* were watched for periods totaling ten daytime hours during times when their gall fig crops were "ripe" and figs, some of which were turning brown, were dropping to the ground. At this stage agaonid wasps were still present in, and emerging from figs on the tree. Although some bulbuls (Pycnonotidae) visited *F. parietalis* and both bulbuls and Brown Fulvettas (*Alcippe brunneicauda*) visited *F. obscura,* no birds were observed to eat gall figs, despite the fact that these birds are known consumers of ripe seed figs of these *Ficus* species. This indicates that birds are able to distinguish the gall figs of these species from their seed figs, which are avidly consumed by a diversity of avian visitors (see Lambert 1989 for a list). No visits by diurnal mammalian consumers were observed. Further evidence of near zero consumption of gall figs was provided by the recovery of (unmarked) fruits from the ground. Of 1154 figs that were counted in one section of a "male" *F. parietalis,* 1128 were later recovered from a plastic sheet placed under that section of tree and cleared of fallen figs daily during the period when they were falling.

The evolution of differences between male and female figs which are recognized by their consumers is undoubtedly of importance in maximizing reproductive potential. While it is important for seed figs to be eaten by dispersal agents and the seeds dispersed, it is equally important that gall figs are not eaten. Not only would agaonid wasps be consumed, but female trees may be deprived of dispersers when they produce figs simultaneously with male trees (Lambert & Marshall 1991 document the fruiting phenology of these *Ficus* species at Kuala Lompat). It is also worth noting that there may be an advantage for female figs to mimic gall figs at an early stage of their development, when being pollinated. Otherwise this might help ovipositing wasps to avoid female trees, which effectively act as traps (S. Compton, pers. comm.).

The rubbery, rather than fleshy texture of gall figs may dissuade frugivorous birds from eating them, and it is also possible that gall figs contain secondary compounds not found in seed figs. It would be interesting to investigate this possibility in future studies. Presumably, the lack of the distinctive color changes usually associated with the ripening of both the seed figs of gynodioecious species, and the figs of most species of monoecious bird-dispersed species (Lambert & Marshall 1991) is a major clue which enables birds to recognize gall figs as being inedible. It is well recognized that frugivorous birds are able to discriminate between fruits using color alone (Gautier-Hion *et al.* 1985), and that they can differentiate between the unripe and ripe fruits of species with distinct preripening colors (Stiles 1982, Willson & Thompson 1982). Although the gall figs of *F. parietalis* and *F. heteropleura* are orange, this is not a color usually associated with ripe fruits eaten by Malaysian birds. Of the 29 bird-dispersed *Ficus* at Kuala Lompat, 17 have figs which are orange prior to ripening, but only two of these species possess ripe figs with orange tones and even these were colored yellow-orange and orange-red rather than pure orange (Lambert 1989).

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