

Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut

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Seed dispersal and pollination by animals play a crucial role in the maintenance of forest ecosystems worldwide. Frugivorous bats are important pollen and seed dispersers in both the Palaeo- and Neotropics, and at least 300 plant species are known to rely on Old World fruit bats (Megachiroptera, Pteropodidae) for their propagation. However, rapid food transit times (generally less than 30 minutes) in frugivorous bats have been thought to limit their ability to disperse seeds to just a few tens of kilometres. Here we demonstrate regular daytime (>12 hours) retention of food and viable fig seeds (*Ficus*, Moraceae) in the gut of the Old World fruit bat *Cynopterus sphinx*: a behaviour not previously reported for any frugivorous bat. Field observations indicate that this behaviour also occurs in other genera. Old World fruit bats are highly mobile and many species undertake considerable foraging and migration flights. Our findings indicate that Old World fruit bats have the potential to disperse small seeds hundreds of kilometres. This necessitates a re-appraisal of their importance in transporting zoochorous seeds to remote areas and facilitating gene flow between isolated populations of plants, both within mainlands and across ocean barriers.

Keywords: long-distance seed dispersal; Megachiroptera; tropical forest regeneration; gut passage; seed germination; *Ficus*

1. INTRODUCTION

Animals play an important role in the dispersal of seed plants worldwide (Ridley 1930; van der Pijl 1982) and are crucial for the flow of plant propagules between isolated habitats (Cox *et al.* 1991; World Conservation Monitoring Centre 1992) and thus for the maintenance of forest ecosystems (Fleming & Heithaus 1981; Marshall 1983; Howe 1984; Whittaker & Jones 1994; Rainey *et al.* 1995). Of almost 1000 bat species worldwide, about 300 feed exclusively or primarily on plant products. Frugivorous bats are important pollen and seed dispersers in both the Palaeo- (van der Pijl 1982; Marshall 1983; Boon & Corlett 1989; Cox *et al.* 1991; Fujita & Tuttle 1991; Utzurrum & Heideman 1991; Mickleburgh *et al.* 1992; Whittaker & Jones 1994; Rainey *et al.* 1995; Eby 1996; Funakoshi & Zubaid 1997) and Neotropics (Fleming & Heithaus 1981). Old World fruit bats (Megachiroptera, Pteropodidae) are highly mobile (Webb & Tidemann 1996) and at least 300 plant species of nearly 200 genera are known to rely on them for either pollination and/or seed dispersal (Marshall 1983; Fujita & Tuttle 1991). Furthermore, these plants produce around 500 economically valuable products (Fujita & Tuttle 1991).

The colonization of remote islands by zoochorous plants has often been attributed almost entirely to birds (Ridley 1930; Docters van Leeuwen 1936; Carlquist 1967; Thornton 1996, p. 115). For instance, van der Pijl (1957) reported a 'peculiar disregard of bats' by early workers (see also Docters van Leeuwen 1936; Whittaker & Jones 1994). Feeding studies of some birds have shown that they can retain viable seeds in their gut for 'maximum' periods sufficient potentially to transport them several thousand kilometres (Proctor 1968). Similar studies of frugivorous bats have tended to report mean or mean *minimum* (our emphasis) food transit times (Fleming & Heithaus 1981; Tedman & Hall 1985; Boon & Corlett 1989; Laska 1990; Utzurrum & Heideman 1991; Eby 1996). Since food transit times in frugivorous bats are generally less than 30 minutes, these studies have lent weight to the assumption that bats are unable to transport seeds across distances exceeding those covered during a typical 30 minute commuting flight (Richards 1990; Whittaker & Jones 1994; Eby 1996; Thornton 1994, 1996, pp. 126, 146; Thornton *et al.* 1996). A striking example of this is the recolonization of post-eruption Krakatau, Indonesia (Verbeek 1884). Although only about 40 km from mainland Java and Sumatra, the role of bats in transporting seeds there has repeatedly been underrated (Docters van Leeuwen 1936; Thornton 1994, 1996), despite the early arrival of bat-dispersed fig trees (*Ficus*, Moraceae) (Docters van Leeuwen 1936; Whittaker & Jones 1994; Thornton 1994, 1996; Thornton *et al.* 1996).

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When studying fruit bats in Indonesia (West Java, Krakatau and Sebesi Island), bats captured around dusk were often observed to defecate dark, viscous faeces, which occasionally contained seeds, and which typically lacked the colour and texture of the fruits eaten that characterizes fresh fruit bat faeces (Thomas 1988). Seventeen bats, almost certainly captured before feeding that day, produced such faeces: seven *Cynopterus sphinx*, three *C. titthaechilus*, two *C. horsfieldi*, four *Rousettus amplexicaudatus* and a single *R. leschenaulti*.

During preliminary captive feeding trials with seven wild-caught *C. sphinx* in Bogor, West Java, bats were observed to defecate before feeding on 16 occasions. These faeces were dark and viscous, resembling those observed in the field, and readily distinguished from the usual faeces of rapidly processed food. We supplied fig seeds with food, since fruit bats regularly consume figs in the wild (Docters van Leeuwen 1936; van der Pijl 1957; Fleming & Heithaus 1981; Fujita & Tuttle 1991; Utzurrum & Heideman 1991; Mickleburgh *et al.* 1992; Whittaker & Jones 1994; Rainey *et al.* 1995; Eby 1996; Funakoshi & Zubaid 1997). These observations of gut-retained food, sometimes voided in up to five or six separate faeces, appeared to explain the occasional occurrence of small numbers (1–7) of fig seeds of a *Ficus* species provided in the previous trial. Seeds of a single *Ficus* species only were used in any one feeding trial (i.e. on any one evening). The seeds of the species used (*F. heterophylla*, *F. ribes*, *F. septica* and *F. variegata*) can be distinguished on the basis of seed-coat texture and seed morphology (unpublished data).

These observations of wild and captive pteropodid bats led us to hypothesize that they retain food in their gut through the day, most probably their last feed of the previous night, and that this retained food may include seeds. We conducted a series of experiments to test this hypothesis.

2. MATERIAL AND METHODS

(a) *Animal housing*

Seven *C. sphinx*, six males and one female, were captured using mist-nets in the Royal Botanic Garden, Bogor (106° 45' E, 6° 36' S). Bats were housed individually in cages (450 mm × 600 mm × 800 mm) in ambient light and temperature conditions (average annual temperature in Bogor is 25 °C; Wernstedt 1972). Cages were sufficient to enable limited flight, since the wingspan of *C. sphinx* is around 400 mm (L. A. Shilton, unpublished data). Water was provided *ad libitum*, and a vitamin and mineral supplemented maintenance diet (cf. Barnard 1995, p. 92) of 150 g of chopped papaya with small amounts of other cultivated fruits was supplied between dusk (18.00) and dawn (06.00). Bats were allowed two weeks to adjust to captivity, before experimental trials commenced. During feeding trials faecal material was collected for examination when uneaten food was removed. At release, 78 days after capture, bats weighed within 1.8% of their capture weight (75.3 ± 13.36 g, mean \pm s.d., $n=7$).

(b) *Do fruit bats retain food throughout the day?*

In the first experiment we conducted seven trials without seeds to test for daytime gut retention of ingested food. Bait was used in three trials; fresh-cut ripe, odorous, papaya was

suspended outside each cage, serving as an olfactory stimulus. Empty feeder bowls were put in position at 18.00, as usual, since the bats may have learnt to associate this act with the availability of food. Food was not supplied to the bats until either all the bats had produced faeces of gut-retained food or until at least midnight (00.00), whichever event came first. We checked for gut-retained faeces each hour. Uneaten food was removed at dawn, and so the duration of food retention was estimated using 06.00 as the latest possible time for food ingestion. We thus report the period of food retention in the gut of *C. sphinx* over and above the approximately 12 h daytime resting period.

(c) *Can seeds be retained in the gut?*

We used seeds of two *Ficus* species, *F. septica* and *F. variegata*, to test whether seeds could be retained in the gut for longer than 12 h. Figs of both *Ficus* species are commonly consumed by *Cynopterus* bats (Thornton 1996; Funakoshi & Zubaid 1997), including *C. sphinx* (L. A. Shilton, unpublished data), in the wild. Both *Ficus* are functionally dioecious, thus figs were picked from a single female (seed-producing) tree of each species. Figs were collected at the same time and stored at 4 °C in a refrigerator for a maximum of 7 d.

Figs were selected for use in trials on the basis of ripeness and the stage of seed development. The small seeds, averaging 1.23 mm in length for both *F. septica* and *F. variegata* (s.d. = 0.08 mm, $n=10$, *F. septica*; s.d. = 0.07 mm, $n=10$, *F. variegata*) (L. A. Shilton and J. M. Watt, unpublished data), were removed from figs and mixed with chopped papaya. A sample of approximately 200 seeds was kept for a control (non-ingested) treatment. Nine trials were conducted with seeds of *F. septica* on five evenings and *F. variegata* on four evenings. On the first two nights the seed content of six *F. variegata* figs (each containing 700–800 seeds) and then 12 *F. septica* figs (each containing 600–700 seeds) were used. The next seven trials used the seed content of 20 figs, providing each bat with the seed content of approximately 2.5 figs. *F. septica* figs were used on four evenings and *F. variegata* figs on three evenings. Faeces of gut-retained food were removed before food was supplied each evening, and rapidly passed faeces were collected at 06.00 the day following the feeding trial. Seeds were separated from faeces by washing in a fine (0.5 mm²) mesh sieve, identified using a binocular microscope and counted.

(d) *Can seeds germinate after retention in the gut?*

In order for zoochorous plants to colonize areas after internal transport, their seeds must be able to germinate after gut passage. We therefore attempted to germinate seeds from the nine feeding trials described in the previous paragraph. Seeds were from three treatments: control (non-ingested), ingested (generally defecated within 1 h) and retained (in the gut >12 h). Seeds were sown on dampened filter paper in sterile Petri dishes under a 12 h light:12 h dark cycle. Seeds from each ingested and retained treatment (replicated across bats) were identified under a binocular microscope before sowing; all retained seeds were of the *Ficus* species provided the previous evening. Each retained seed was sown, as numbers were small (1–118 seeds in faeces of gut-retained food), whereas a random subsample of approximately 200 seeds was sown from control and ingested treatments (table 1). High moisture content was maintained in Petri dishes by regular watering. Germination was recorded as the extension of the hypocotyl more than 1 mm beyond the exocarp (cf. Murphy *et al.* 1993). Each germinated seed was counted and removed at approximately 3-day intervals. We used the

Table 1. *Probabilities of germination of Ficus septica and F. variegata seeds*

(Probabilities of germination, from logistic regression analysis, of control (non-ingested), ingested (generally defecated within 1 h) and retained (in the gut >12 h) *F. septica* and *F. variegata* seeds supplied to seven *Cynopterus sphinx*. Mean germination probability is shown with lower and upper 95% confidence intervals in square brackets. Large confidence intervals for retained seeds are due to small seed numbers.)

seed treatment	no. of samples	no. of seeds	germination probability
<i>Ficus septica</i>			
control	9	212.1 ± 107.9	0.38 [0.33,0.44]
ingested	35	246.5 ± 113.4	0.51 [0.48,0.54]
retained	26	10.9 ± 23.3	0.41 [0.27,0.57]
<i>Ficus variegata</i>			
control	6	202.2 ± 40.3	0.94 [0.91,0.97]
ingested	28	224.3 ± 47.5	0.93 [0.91,0.94]
retained	17	9.2 ± 12.4	0.99 [0.70,0.99]

proportion of seeds that had germinated by day 28 in analysis, since 95% of seedlings of these *Ficus* species that germinated from topsoil samples from Krakatau did so within 29 days of sowing (Whittaker *et al.* 1995).

(e) Statistical analyses

Logistic regression analysis was conducted to estimate and test treatment effects on seed germination probability, at day 28, in both *Ficus* species. Heterogeneity between trials, and between bats in trials (dispersion parameter = 7.251 for *Ficus septica* and 4.540 for *F. variegata*) was adjusted for by using variance ratio statistics. Statistical computation was done using GenstatTM 5 Release 3 (Genstat 5 Committee 1993).

3. RESULTS

(a) Daytime gut retention of food

Bats became active shortly before dusk, making frequent short flights within their cage. This activity did not induce defecation, which occurred between dusk and 01.00 (>12 h to >18 h gut retention). Furthermore, the time of defecation was not accelerated by the presence of odorous bait on three nights. Retained food was voided 1–3 h after dark (>12 h to >15 h gut retention) by at least five of the seven bats on these three evenings, and 6.6 ± 0.8 bats produced retained faeces in the seven trials. We concluded that these fruit bats regularly, perhaps routinely, retain ingested food in the gut from one night to the following evening.

(b) Daytime gut retention of ingested seeds

When the seed content of six *F. variegata* and 12 *F. septica* figs was supplied to the seven bats, seeds were present in the gut-retained faeces of one bat and three bats, respectively. When the seed content of 20 figs was supplied, seeds were present in 79.6% of retained food faeces in these seven trials. Food was retained >12 h in the gut of 6.78 ± 0.4 bats in the nine trials, compared with 6.6 ± 0.8 bats in the seven trials without seeds. Thus, ingestion of seeds did not affect whether food was retained in the gut,

and despite relatively low provisioning of seeds in these experiments, compared to the number of figs and seeds that might be ingested in the wild (cf. Morrison 1980; Thomas 1984), bats frequently retained seeds of *F. septica* and *F. variegata* in the gut for >12 h (5.6 ± 0.8 bats, $n=7$). In several instances, food and seeds were retained >18 h.

(c) Seed germination

Table 1 shows the mean germination probabilities of control, ingested and retained seeds with lower and upper 95% confidence intervals. The two species germinated at very different levels, with *F. septica* germination probability being consistently lower than *F. variegata*, and there was a significant ($p=0.004$) difference between treatments within *Ficus* species. Treatment effects were significant in *F. septica* ($p<0.001$), but there was no treatment effect in *F. variegata* ($p=0.12$).

Seeds retained in the gut of *C. sphinx* >12 h germinated at least as well as non-ingested control seeds in both *Ficus* species. Thus, although confidence intervals are large due to the small seed numbers in this treatment, gut retention of these small *Ficus* seeds does not appear to adversely affect seed viability, and seeds retained in the gut >12 h have the potential to germinate and establish after gut passage.

4. DISCUSSION

Frugivorous bats have an unusual mode of fruit processing by which the fruit is largely handled externally: the fruit pulp is squeezed between the palate and the tongue to extract and ingest the juice (Morrison 1980; Thomas 1984; Bonaccorso & Gush 1987; Charles-Dominique 1991). Despite external fruit handling, frugivorous bats have been reported to swallow as much as 80% of the tiny seeds of figs (Morrison 1980). Only small seeds are ingested by frugivorous bats as the gastrointestinal tract of frugivorous bats is narrow (Docters van Leeuwen 1935; Boon & Corlett 1989; Richards 1990). Seeds up to a maximum of 5 mm may be ingested by *Pteropus conspicillatus*, the spectacled flying-fox, since the anterior lumen of the oesophagus is about 5 mm in diameter in this species (Richards 1990). *P. poliocephalus*, the grey-headed flying-fox (700–950 g), ingested seeds up to a maximum size of 4.2 mm during captive feeding studies (Eby 1996). The gullet of some *Cynopterus* species is 2–2.5 mm in diameter (Docters van Leeuwen 1935). Thus, *Cynopterus* bats may be expected to spit out seeds greater than 2.5 mm. *C. brachyotis*, the lesser dog-faced fruit bat, ingested and dispersed seeds of 2.3 mm in greatest diameter in Singapore (Boon & Corlett 1989).

Fleshy fruits, including figs, are often low in protein and lipids, but high in carbohydrates (e.g. Martínez del Rio & Restrepo 1993; Conklin & Wrangham 1994). Frugivorous bats generally consume large quantities of fruit each night, often in excess of their own body mass (Morrison 1980; Thomas 1984, 1988; Izhaki *et al.* 1995), and thus must pass digesta rapidly through the gut. Various studies have documented rapid food transit times, frequently of less than 30 min, and usually less than 1 h, between food ingestion and the initial defecation in frugivorous bats (Docters van Leeuwen 1935; Nelson 1965; Morrison 1980; Fleming & Heithaus 1981; Utzurrum

1984; Tedman & Hall 1985; Boon & Corlett 1989; Laska 1990; Charles-Dominique 1991; Utzurrum & Heideman 1991; Eby 1996), with passage times largely unaffected by the fruit being eaten (Richardson *et al.* 1987).

Laska (1990) reported mean gut-passage times of 22 min in *Carollia perspicillata* to 34 min in *Phyllostomus discolor*. In Old World fruit bats gut-passage times have been reported to be similarly rapid (Docters van Leeuwen 1935; Utzurrum 1984; Tedman & Hall 1985; Boon & Corlett 1989; Utzurrum & Heideman 1991; Eby 1996). Utzurrum & Heideman (1991) reported gut-passage times of 20–45 min in *Nyctimene rabori* and *Ptenochirus jagori* fed on ripe *F. chrysolepis* figs. Boon & Corlett (1989) reported gut-passage times of 11–15 min in captive *C. brachyotis* that averaged 37 g in body mass. Although Richardson *et al.* (1987) found *C. brachyotis* and *Pteropus vampyrus* to have mean gut-passage times of 7.5 h and 5.5 h, respectively, they concluded that both species had an extremely rapid passage of food, with tiny polymer bead markers first appearing within 30 min of ingestion.

As far as we are aware, the behaviour of retaining food in the gut through the daytime resting phase has not previously been reported for any frugivorous bat. Laska (1990), in his study of gut passage in three frugivorous phyllostomid species (*Carollia perspicillata*, *Phyllostomus discolor* and *Sturnira lileum*), found no evidence for daytime food retention. However, it is conceivable that the use of a chocolate-brown food dye to mark ingested food (banana) could have masked whether initial defecations were of gut-retained food, since these defecations are characteristically dark. Furthermore, gut retention of food during the daytime rest phase could also explain observations such as those of Charles-Dominique (1991, p. 248) of *C. perspicillata* producing the first defecation just 5 min after ingestion of food, in the beginning of the evening when the bat is very active. Since digestive efficiency is often low in fruit bats (e.g. Morrison 1980; Thomas 1984; Tedman & Hall 1985), the behaviour of retaining food in the gut during the daytime resting phase may enable increased nutrient assimilation from the last feed, and thus confer a nutritional benefit to the bat.

Seeds retained in the gut of *C. sphinx* for >12 h, could potentially be dispersed to areas over 300 km from the parent plant, if the bats were to fly continuously at 25 km h⁻¹ (the speed at which they commute over water; L. A. Shilton and C. Tidemann, unpublished data). Since dispersal events do not need to be frequent to be effective (Carlquist 1967), seeds retained in the gut in this way may be sufficient to establish populations of plants in remote areas. Although migratory flights have not, to our knowledge, been reported for *C. sphinx*, many species of Old World fruit bat are known to undertake seasonal migrations (e.g. Ratcliffe 1931; van der Pijl 1957; Marshall 1983; Thomas 1983; Eby 1996) and demonstrate extensive nomadic behaviour (e.g. Nelson 1965; Webb & Tidemann 1996) in a number of regions. Large *Pteropus* species may commute distances up to 50 km (van der Pijl 1957) during their nightly searches for food patches at speeds of 40 km h⁻¹ (Richards 1990). Furthermore, it is well documented that frugivorous bats defecate during flight (e.g. Docters van Leeuwen 1935; Boon & Corlett 1989),

and this behaviour has been observed in *Cynopterus* spp., *Rousettus amplexicaudatus* and *Pteropus vampyrus* in Indonesia, and *Pteropus poliocephalus* in Australia (personal observation). Furthermore, *P. poliocephalus* captured around dusk, before foraging, at a camp devoid of food resources (C. Tidemann, personal communication), defecated retained food (L. A. Shilton, personal observation), suggesting that the behaviour of retaining food in the gut during the daytime rest phase may be widespread in Megachiroptera.

On Krakatau, *Cynopterus* bats were observed to commute over water between islands (2–5 km) around dusk (personal observation), indicating that these small pteropodid bats may transport gut-retained seeds to new localities. Furthermore, the early arrival of *Cynopterus* spp. on Krakatau after the volcanic sterilization of the islands in 1883 provides evidence for longer movements by these bats, since the nearest source for the colonists are the islands Sebesi and Sebu (12 and 20 km from Krakatau, respectively) (Thornton 1996; Whittaker & Jones 1994).

The role of *Pteropus* species in localized seed dispersal and pollination in the South Pacific Islands has led to the hypothesis that these animals may be of key importance in maintaining the structure of these ecosystems, where there is a paucity of other vertebrate frugivores (Cox *et al.* 1991; Rainey *et al.* 1995). Our findings indicate a greater role for Old World fruit bats in long-distance dispersal of small seeds than has been thought possible, highlighting both the importance of further research on these animals and the value of conserving them in a world where forest habitats are becoming increasingly fragmented.

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