BIOTROPICA 32(4a): 759–764 2000

Fig-Eating by Bornean Tree Shrews (*Tupaia* spp.): Evidence for a Role as Seed Dispersers[1]

Key words: *Borneo;* Ficus; *frugivory; germination; gut passage time; Scandentia; seed dispersal.*

FRUIT-EATING VERTEBRATES ARE AN IMPORTANT COMPONENT of tropical forests, where a large number of plant species depend on them for seed dispersal (Howe & Smallwood 1982). By facilitating the regeneration of vegetation and thus maintaining biodiversity, seed dispersers also have a role in ameliorating anthropogenic effects on tropical forests. While birds, fruit bats, and primates are perceived as being the most important seed dispersers (Ridley 1930, van der Pijl 1982, Howe 1986), the role of small non-volant mammals also may be prominent (Price & Jenkins 1986, Julien-Lafferiere 1993, Compton *et al.* 1996, Forget 1996).

[1] Received 26 March 1999; revision accepted 27 September 1999.

TABLE 1. Ficus *species at which tree shrews were observed eating figs (●). Fig tree growth forms: FST = freestanding tree; C = climber; HE = hemi-epiphyte (strangler). Tree shrew nomenclature follows Corbet and Hill (1992).* Ficus *taxonomy follows Corner (1965).*

Ficus species	Fig diameter (mm; $\bar{x} \pm$ SD)	Growth form	Large tree shrew (*T. tana*)	Lesser tree shrew (*T. minor*) and slender tree shrew (*T. gracilis*)	Common tree shrew (*T. glis*)
F. acamptophylla	11.5 ± 2.03	C		●	
F. benjamina	11.5 ± 1.26	HE		●	
F. consociata	12.9 ± 1.45	HE		●	●
F. dubia	22.5 ± 1.54	HE		●	
F. fulva	12.8 ± 0.621	FST	●	●	
F. kerkhovenii	11.1 ± 0.49	HE		●	●
F. pisocarpa	11.9 ± 0.603	HE		●	●
F. subgelderi	14.9 ± 0.88	HE		●	
F. sumatrana	13.7 ± 0.943	HE		●	●
F. treubii	14.9 ± 1.04	FST	●		

The potential for tree shrews (order Scandentia, family Tupaiidae, with all 19 species confined to eastern Asia; Wilson & Reeder 1993) to act as seed dispersers remains largely unknown, despite their abundance, diurnal feeding behavior, and partially frugivorous diet (Ridley 1930, van der Pijl 1982, Emmons *et al.* 1991). Emmons (1991) described the feeding behavior and food transit times of two Bornean species (*Tupaia tana* Raffles and *T. minor* Günther), but surprisingly, failed to address the potential role of tree shrews in seed dispersal. Seven of the 11 types of fruit she observed being eaten by tree shrews were from species of fig trees (*Ficus*, Moraceae), a genus for which its dietary importance also has been highlighted in other accounts of tree shrew biology (*e.g.*, Kawamichi & Kawamichi 1979). Records of frugivory, however, are insufficient to confirm that tree shrews disperse fig seeds because frugivores may act as seed predators (*sensu* Janzen 1971), destroying most or all of the seeds inside the fruits they eat.

In this paper, we present quantitative data from a Bornean lowland rain forest on fig frugivory by four species of tree shrews (large tree shrew, *T. tana* Raffles; common tree shrew, *T. glis* Diard; lesser tree shrew, *T. minor* Günther; and slender tree shrew, *T. gracilis* Thomas). Additionally, we describe for the first time the effects of ingestion by tree shrews on the survival and germination rates of fig seeds. Our results show that these mammals can be effective seed dispersers.

Fieldwork was conducted in 1997 and 1998 in the mixed dipterocarp forest of Lambir Hills National Park, Sarawak, Malaysia (4°20′N, 113°50′E), as part of a larger study on frugivory and seed dispersal of *Ficus* species. The park is composed largely of mixed dipterocarp forest with high botanical diversity (Ashton & Hall 1992, LaFrankie *et al.* 1995). Each ripe crop was observed over three days for a total of six hours between 0600 and 1000 h. Observation sessions lasted one to three hours and were divided into five-minute scan periods during which the identities and group sizes of all feeding frugivore species were recorded. Additionally, opportunistic focal animal observations (*sensu* Altmann 1974) allowed feeding rates and visit durations to be assessed. During scan and focal samples, the foraging heights of the tree shrews were classed as shrub layer (0–2.5 m), understory (2.5–12.5 m), subcanopy (12.5–27.5 m), canopy (27.5–42.5 m), or emergent (>42.5 m), following the classification of Yamakura (1992).

Because the lesser tree shrew (*T. minor*) and the slender tree shrew (*T. gracilis*) could be confidently distinguished only on the basis of cranial or foot measurements (Payne *et al.* 1985), all field data pertaining to these two species were pooled. The ten *Ficus* species fed upon included freestanding trees, hemi-epiphytes (strangler figs), and a climber (Table 1). The fruit of these species varied in diameter from those of *F. kerkhovenii* ($\bar{x} \pm$ SD; 11.1 ± 0.49 mm) to those of *F. dubia* (22.5 ± 1.54 mm). Feeding visits were generally short (<5 min; Table 2), and tree shrews only were observed foraging singly, removing small numbers of figs before leaving the fruit crop. Tree shrews foraged in all vertical strata of the forest with the exception of the emergent layer. While *T. glis* and *T. minor*/*T. gracilis* foraged in all strata between the understory and the canopy, *T. tana*, reported previously to be a largely

TABLE 2. *Feeding behavior of tree shrews during focal observations. Foraging height classes are abbreviated as follows: SL = shrub layer; US = understory; SC = subcanopy; C = canopy.*

Tree shrew species	Foraging heights	*N* observations	Visit duration (min; $\bar{x}$ ± SD)	Feeding rate as (figs/min; $\bar{x}$ ± SD)
T. tana	SL, US	5	3.77 ± 0.863	1.01 ± 0.06
T. gracilis/*T. minor*	US, SC, C	6	3.55 ± 1.32	0.71 ± 0.29
T. glis	US, SC, C	7	2.7 ± 0.918	1.08 ± 0.35

terrestrial species (Payne *et al.* 1985), was observed only at lower levels in the forest (Table 2). Figs were consumed at a mean rate of *ca* 1/min, although the variability in fig size among species (Table 1) was not taken into account when calculating mean feeding rates. Such short feeding visits and low fruit removal rates suggest rapid satiation (a possible function of the tree shrews' small size: *T. minor,* 30–71 g; *T. gracilis,* 60–98 g; *T. tana,* 154–305 g; Payne *et al.* 1985), fear of predation, or preference for alternative food items.

In addition to tree shrews, the majority of the fig crops attracted many other frugivores, most notably birds and arboreal squirrels (*Callosciurus* spp.). The contributions of tree shrews to total fruit removal recorded during scan samples were low relative to those of these other mammalian and avian fig eaters. This, however, may not be the case with fruit removal of *F. treubii.* This species is geocarpic, presenting its fruit on ground-level runners and thereby failing to attract the diverse assemblages of frugivorous birds observed at the other species in this study. The large tree shrew was the only frugivore directly observed eating figs of *F. treubii,* although indirect evidence based on feeding signs (tracks and dental impressions in discarded fig portions) suggested that nocturnal murid rodents and mouse deer (*Tragulus* spp.) also ate them.

Details of tree shrew gut passage times and the effects of ingestion on fig seeds could not be determined in the field. The effects of gut passage on fig seed survival and germination rates therefore were investigated using a pair of captive-born lesser tree shrews (*T. minor*) maintained at Roundhay Tropical World, Leeds, England. The animals, both males, were housed in a 2- × 1- × 1-m cage, furnished with climbing apparatus and two nest boxes. Female figs of *F. montana* Burm. F. were harvested from experimental fig tree and fig wasp greenhouse populations maintained at the University of Leeds. *Ficus montana* is a small dioecious epiphytic shrub native to southeast Asia with females that produce figs in leaf axils and on stems up to *ca* 2 m above ground level. Fruits reach *ca* 18 mm in diameter and turn bright red at maturity. While *F. montana* is sympatric with *T. minor* in lowland Borneo and Peninsular Malaysia, it was absent from the field site (Corner 1965; Payne *et al.* 1985; R. Harrison, pers. comm.). The size, color and placement of the figs of *F. montana* suggested that they were likely to be fed on by a wide variety of understory and ground-feeding solitary or small-group foraging species such as bulbuls, barbets, flower-peckers, tree shrews, and squirrels (Shanahan & Compton in press).

To determine tree shrew gut passage times, we fed each animal enough freshly picked figs to satiate them temporarily (5–8 figs; wet mass $\bar{x}$ ± SD = 0.55 ± 0.21 g) prior to providing them with their usual diet of chopped grapes, banana, and live crickets. Then the time between initial feeding and the appearance of the first seed-bearing defecation from each animal was recorded. To investigate effects of ingestion on germination, we placed 100 seeds each from feces and from control figs in petri dishes on moist filter paper at 23°C, with an 18-h light/6-h dark artificial light regime. This temperature and light regime produces optimal germination rates for control seeds of *F. montana.* The experiment was performed twice, and to control for between-tree differences in seed germination (*e.g.*, Lieberman *et al.* 1979), all figs in each of the two trials were gathered from the same parent, with some fed to the subject animals and some retained as uneaten controls.

Feeding behavior in captivity resembled that observed by Emmons (1991), with the figs picked up by the mouth or forefoot and carried in the mouth to a feeding site on a branch. Upon coming to rest, the animals held the fig in one forefoot and nibbled rapidly at the flesh, often turning the fig inside out and eating the seed-rich core first. Individual fruits were ingested entirely in about one minute ($\bar{x}$ ± SD = 63.1 ± 14.0 sec; N = 22). In contrast to Emmons' (1991) findings, discarding of seeds or the fig coat was not observed, small numbers of seeds being dropped in only 3 of 47 observed feeding events.

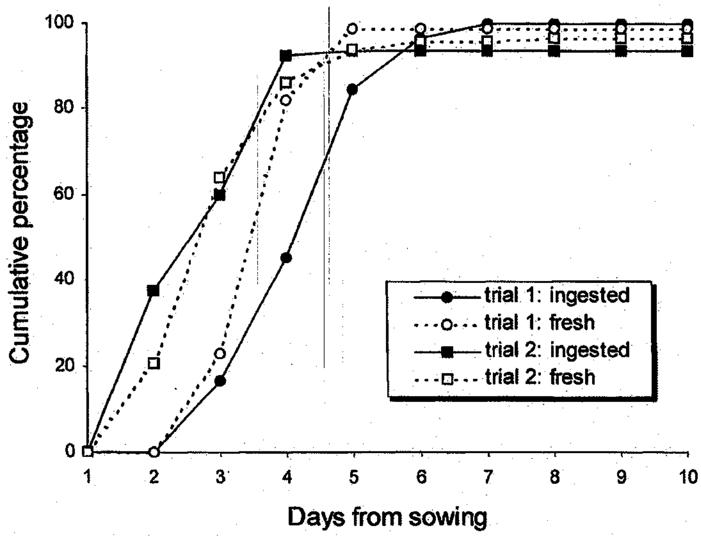

FIGURE 1. Cumulative percentage seed germination over time for tree shrew-ingested and control (fresh) seeds. In each trial, 100 seeds were sown.

This feeding behavior contrasted with that of *Callosciurus* squirrels (the other non-volant mammals commonly observed eating figs at our field site), which tended to act as "pulp thieves" (Howe & Vande Kerckhove 1981) by eating only the figs' fleshy portion and dropping the seed core (Lambert 1989; M. Shanahan, pers. obs.). *Ficus* species have small seeds (length <3 mm, diameter ≤1.5 mm among the species referred to in this paper), which improves their likelihood of ingestion by tree shrews, because larger seeds often are masticated (Emmons 1991).

Seed-bearing feces were defecated from 33 ± 2 to 63 ± 11 min after fig ingestion (minimum and maximum $\bar{x}$ ± SD; N = 10), and each dropping contained 60.6 ± 33.9 ($\bar{x}$ ± SD) seeds. Defecation occurred from branches rather than on the ground, with the animals tightly gripping the branch with all four feet and curving the back so that feces dropped to the ground below. Under natural conditions, feces evacuated in the canopy are likely to be intercepted by tree branches, a condition favoring the establishment of seeds belonging to hemi-epiphytic fig species. Within five to seven days, 94–100 percent of the ingested seeds germinated (Fig. 1). No difference was found in germination frequency between ingested and control seeds (trial one: Yates' correction $\chi^2[1] = 2.14$, $P > 0.05$; trial two: $\chi^2[1] = 1.52$, $P > 0.05$; total: χ^2 [1] = 0.174, $P > 0.05$). Germination rates of ingested and control seeds, however, did differ, but in different directions in the two trials (trial one: $D = 0.373$, $P < 0.05$; trial two: $D = 0.186$, $P < 0.05$; two-sample Kolmogorov-Smirnoff tests; Sokal & Rohlf 1995). In trial one, control seeds germinated more rapidly than those that were ingested $\bar{x}$ ± SD = 3.93 ± 0.64 compared to 4.59 ± 1.02 d); in trial two, control seeds germinated more slowly $\bar{x}$ ± SD = 2.27 ± 1.03 and 1.97 ± 0.90 d, respectively). The fig seeds therefore passed largely undamaged through the gut of *T. minor,* but did not consistently germinate more quickly.

The effectiveness of frugivores as seed dispersers is determined by both qualitative and quantitative components (Schupp 1993). In terms of quantity, the propensity of tree shrews for fig eating has been documented (Kawamichi & Kawamichi 1979, Emmons 1991); however, their relative contributions to fig seed removal at our field site were low, suggesting either low population densities relative to other frugivores or that other food sources such as invertebrates or other fruit were more attractive. Relative contributions to the dispersal of geocarpic fig species, which do not utilize avian frugivores, may be higher but remain to be quantified. Other factors influencing the quality of seed dispersal include where seed-containing feces are deposited and the treatment they receive during transport. Tree shrews forage in all vertical strata from the forest floor to the canopy, and potentially deposit seeds in favorable locations for ground-germinating climbers, freestanding trees, and the canopy-germinating hemi-epiphytic strangler fig trees. Furthermore, the rapid satiation of the tree shrews appeared to necessitate frequent short feeding visits to fruiting trees, which increased the likelihood of seeds being voided away from their parent trees.

The high survivorship of the fig seeds passing through the gut of *T. minor* contrasted with that seen when fig seeds were eaten by other small, non-volant mammals (*e.g.*, rodents; *e.g.*, Compton *et al.* 1996) and *Treron* fruit pigeons (Cowles & Goodwin 1959, Lambert 1989). The more delicate treatment of seeds by tree shrews is likely a function of their relatively rapid seed passage times and simple guts, which resemble those of fruit bats (Emmons 1991). With seed transit times of up to an hour or more and daily movements of between hundreds and thousands of meters (Emmons *et al.* 1991), tree shrews are a potentially important, but largely overlooked, group of dispersers for small seeds in the forests of tropical Asia.

Fieldwork was conducted with permission of the Forest Department Sarawak, for which thanks are due to the Director of Research, Abang Haji Abdul Hamid. Work in Sarawak was facilitated by a research fellowship from the Institute of Biodiversity and Environmental Conservation; thanks to Dr. Stuart Davies and Prof. Ismail Ghazally at UNIMAS. Field identifications of *Ficus* individuals were made by Rhett Harrison of Kyoto University during his doctoral research. We are grateful to M. Inwood and staff at Roundhay Tropical World (Leeds) for permission to study the tree shrews there. J. Moore, J. Wong, T. Fleming, and three anonymous reviewers provided helpful comments on an earlier draft of the manuscript. This study was funded by a States of Jersey Education Committee research grant to MS.

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