# A preliminary study of bird use of fig *Ficus* species in Amurum Forest Reserve, Nigeria

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**Summary**

While fig trees (*Ficus*: Moraceae) are acknowledged as keystone resources for frugivore communities in tropical forests, their detailed use by frugivores is often poorly understood. In this study, we found over 400 fig trees of 12 species in Amurum Forest Reserve, Nigeria. We analyse bird visits to 12 individual trees of eight *Ficus* species, observed over a two-year period (2007–9), during which we recorded 3234 visits by 48 bird species. Different fig trees received between 23 and 826 visits during our observations; the diurnal pattern of visits was similar for all fig species, with clear morning (8h00–9h30, larger) and late afternoon (16h00, lesser) peaks, with a lull in visits around mid-day. Mean visit duration varied between 2.9 ± 1.8 min. and 20.5 ± 19.2 min. (mean ± SD) at different fig species. Birds ate between 1.7 ± 1.1 and 5.2 ± 4.4 figs per visit at different fig species. Our study provides preliminary information on *Ficus*–bird associations and confirms that figs are important resources for frugivorous birds in Amurum Forest Reserve. We suggest that at least four *Ficus* species provide disproportionately important resources for frugivorous birds: *F. lutea*, *F. ingens*, *F. thonningii* and *F. abutilifolia*.

**Résumé**

**Étude préliminaire de la consommation par les oiseaux de figues *Ficus* spp. dans la Réserve de la Forêt d'Amurum, Nigeria.** Bien que les figuiers (*Ficus*: Moraceae) soient reconnus comme étant des ressources-clé pour les communautés de frugivores dans les forêts tropicales, leur consommation par les frugivores n'est souvent pas connue avec précision. Dans cette étude, nous

avons trouvé plus de 400 figuiers dans la Réserve de la Forêt d'Amurum, Nigeria. Nous analysons les visites par les oiseaux de 12 arbres appartenant à huit espèces de *Ficus*, observées sur une période de deux ans (2007–9), durant laquelle nous avons noté 3234 visites par 48 espèces d'oiseaux. Les différents figuiers ont reçu entre 23 et 826 visites pendant nos observations; le scénario diurne des visites était le même pour toutes les espèces de figuiers, avec des pics évidents pour le matin (8h00-9h30, le plus important) et la fin d'après-midi (16h00, moins important), avec une pause dans les visites autour de la mi-journée. La durée moyenne des visites aux différentes espèces de figuiers variait entre 2,9 ± 1,8 min. (moyenne ± sdv). Les oiseaux consommaient entre 1,7 ± 1,1 et 5,2 ± 4,4 figues par visite aux différentes espèces de figuiers. Notre étude fournit de premières informations sur les associations *Ficus*–oiseaux et confirme que les figues sont des ressources importantes pour les oiseaux frugivores dans la Réserve de la Forêt d'Amurum. Nous suggérons qu'au moins quatre espèces de *Ficus* fournissent des ressources très importantes pour les oiseaux frugivores: *F. lutea*, *F. ingens*, *F. thonningii* et *F. abutilifolia*.

## Introduction

Fig trees (*Ficus*: Moraceae) provide reliable dietary resources for frugivores including birds in tropical forests (Walker 2007), and birds play important ecological roles dispersing fig seeds (Peh & Chong 2003), thus contributing to the maintenance of species diversity (Snow 1981, Wenny & Levey 1998, Holbrook & Smith 2000). Several criteria have been used to define keystone plant species for frugivores including phenology (*e.g.* fructification during periods of general fruit scarcity: White 1994), reliability of fruit production (Leighton & Leighton 1983, Terborgh 1986), abundance of fruit produced (Bond 1993, Peres 2000), and most commonly, population size of frugivores that use specific resources (Peres 2000). Fig trees are well known as a key component of fruit resources in tropical forests (Lambert & Marshall 1991, Shanahan *et al*. 2001, Bleher *et al*. 2003). Over 10% of the world's birds and 6% of mammals consume figs, making *Ficus* the most widely consumed plant genus (Shanahan *et al*. 2001). Despite the long interest in mutually beneficial fig-frugivore interactions (*e.g*. Wheelwright 1985), most fig-frugivore studies have been restricted to the Neotropics and southeast Asia, commonly with limited sample size (number of fig species monitored) and observation period (1–2 weeks) (*e.g.* Shanahan *et al*. 2001, Ragusa-Netto 2002, Bleher *et al*. 2003, Peh & Chong 2003, Tello 2003). In Africa south of the Sahara, *c*. 112 *Ficus* species are recognised, with southern Africa being the centre of diversity (Berg & Wiebes 1992); but detailed information on fig-frugivore interactions is scarce. Long-term research might identify keystone *Ficus* and frugivore species to be prioritised in conservation efforts (Bleher *et al*. 2003).

We report here a two-year study on birds visits to *Ficus* species in Amurum Forest, Nigeria. Amurum holds 278 bird species, 31% of the total recorded in Nigeria, underpinning its status as an "Important Bird Area" and one of Nigeria's key avian biodiversity hotspots (Ezealor 2001) and, therefore, a suitable area to explore fig-bird interactions. We evaluated visit patterns of birds on eight fig species. Our main objective was to identify key frugivores visiting *Ficus* species and potentially guide future conservation programmes in Nigeria. We expected that visitors to a putatively critical food resource would mainly visit for foraging. Thus, we assessed the importance of the various fig species by recording all visits by birds, the time spent by visitors on each tree and the number of figs eaten; we also noted temporal feeding patterns and visitor behaviour on the tree.

## Methods

The study was conducted in Amurum Forest Reserve at *c*. 1300 m altitude on the Jos Plateau in north-central Nigeria (9°52′30″N, 8°58′30″E). The reserve, which covers *c.* 300 ha, is a typical savanna woodland dominated by grasses, with scattered rocky outcrops, and strips of riparian forest along streams (Vickery & Jones 2002). In the grassland savanna, common trees and shrubs include *Dichrostachys cinerea*, *Jasminum dichotomum*, *Combretum fragrans* and *Piliostigma thoningii*. The rocky outcrops are characterised by *Parkia biglobosa*, *Acacia ataxacantha* and several *Ficus* species, whereas the most frequent woody plant species in the forest patches are *Boscia angustifolia*, *Harungana madagascariensis*, *Syzygium guineense* and *Ochna schweinfurthiana* (Gofwen 2009). Temperatures in the region are 8–15°C during the coldest months (November–February) and rise to 30–38°C during the warm and dry months (March–April). Mean annual rainfall is 1411 mm, falling mainly between April and October (Payne 1998).

Of the 278 bird species known from Amurum Forest Reserve, at least 58 are, to varying extents, fruit feeders. We here follow Snow (1971) in using "fruit" to mean fleshy fruit. Based on Brown *et al*. (1982), Fry & Keith (2004) and Fry *et al*. (1988, 2000), we classified these 58 species into three main categories: obligate frugivores (18 species) that feed primarily on fruit, partial frugivores (28 species) which have, beside fruits, other major food items (*e.g*. invertebrates), and opportunistic fruit-eaters (12 species) that occasionally eat fruit; in this study we recorded 48 of these 58 species (Table 1). Nomenclature of birds follows Borrow & Demey (2001).

We determined *Ficus* density and diversity in 25 plots of 200 × 200 m (Fig. 1), selected across the reserve using computer-generated random numbers. In each plot, *Ficus* trees were photographed and identified to species level (where possible), the number of trees of each species was counted, and their geographical coordinates taken, allowing us to map their spatial distribution. Keay (1989) and the Fig Web (<www.figweb.org>) were used for species identification.

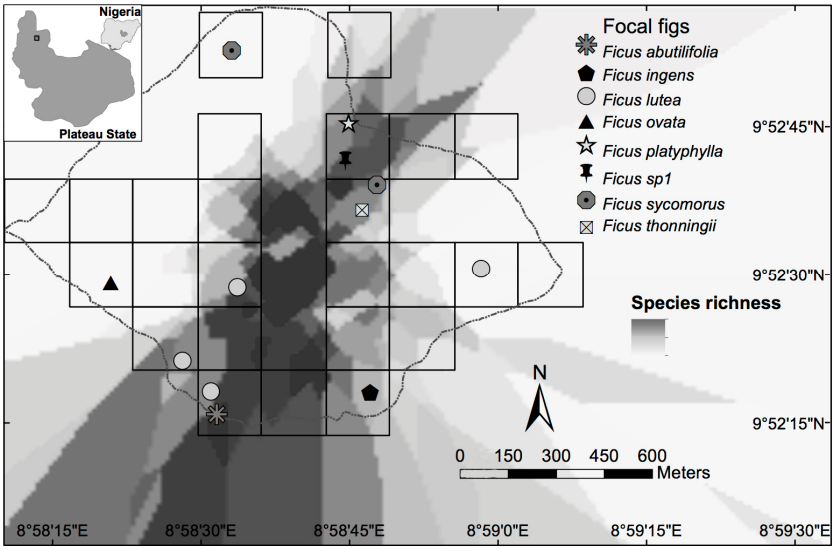


**Figure 1. Map of Amurum Forest Reserve showing *Ficus* species richness. The Reserve is the diamond-shaped area. Depth of shading reflects interpolated values of fig species richness from high (dark) to low (light) derived from species richness in the 25 plots using Ordinary Kriging with a 12-cell neighbourhood. The 25 plots are indicated and locations of the 12 *Ficus* trees observed for bird frugivory are shown. Inset: the reserve's position in Plateau State and Nigeria.**

Over a two-year period March 2007 to June 2009, we observed bird–fig interactions at 12 individual trees of eight fig species (four trees of *F. lutea*, two of *F. sycomorus*, and one each of *F. abutilifolia*, *F. thonningii*, *F. ingens*, *F. ovata*, *F. platyphylla* and an unidentified *Ficus* species) when they were found fruiting during this period (Fig. 2). Each focal tree was found in fruit once during the study period and observations commenced when the tree was first noted to be fruiting. Hence, we could not be certain of the overall length (in days) of fruiting period, nor did we estimate the number of figs produced by each tree during a fruiting event. For all birds visiting a tree, we recorded the following: species identity and number, time spent in the tree (including eating, perching and moving within the tree), number of figs eaten and handling behaviour. Independence of observations was not assured as birds were not marked: individual birds repeatedly revisiting the same tree would have been classed as different observations. We acknowledge that this may have caused pseudo-replication, but judging from observations of different individuals visiting concurrently, and considering the extended study period, we believe the data

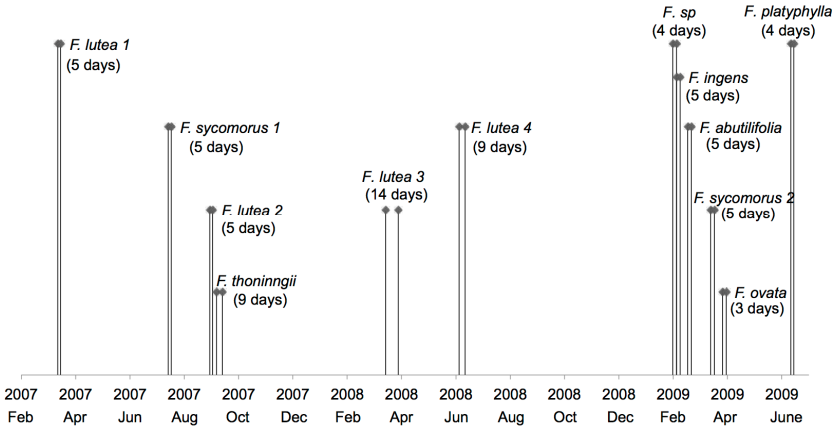


**Figure 2. Chronology of observation of bird-fig interactions in Amurum Forest Reserve, Nigeria. The perpendicular lines mark first and last observation day for each tree, and their length is arbitrary to enable legibility. N days in brackets are total observation days on each tree.**

on fruit-feeding behaviour to be reliably indicative of true patterns. Visitation was recorded by scan-sampling from a concealed position using binoculars and telescope. Observations consisted of 12 h sessions (6h00–18h00), lasting from the time of ripening of figs on an individual tree through to consumption of the last figs on it, following the method of Tello (2003). We collected quantitative data on visit time (seconds spent on a tree) and fig consumption (number eaten per visit), and also recorded the temporal patterns of visits and the behaviour of visiting birds.

A preliminary analysis showed that foraging activity of frugivores occurred mainly between 6h00-11h00 and 13h00-18h00, with lower activity in the afternoon. We therefore explored the differences between morning (6h00–11h00) and afternoon (13h00–18h00) in the number of figs eaten, time spent on each tree, and number of visits to each tree, using the non-parametric two-sample Kolmogorov-Smirnov test. We also investigated intra-specific differences among individual trees of *Ficus lutea* by analysis of variance (ANOVA), contrasting mean time spent per visit, mean number of figs eaten per visit and number of visits by different bird species, between individual trees (n = 135, 229, 302, 308 for the four trees; sample sizes are the subsets of visits where fig consumption was observed) using Tukey's honest significant difference (HSD). To assess whether these three variables were correlated, we calculated the correlation coefficient and determined its significance using Pearson's product-moment method. Prior to this correlation test, variables were $\log_{10}$-transformed to meet the assumptions of normality and homogeneity of variance.

Finally, we explored the temporal dynamics of tree usage by frugivores. All analyses were carried out using R (<http://www.R-project.org> consulted 2013). All mean values are reported as mean ± 1 standard deviation.

## Results

### Fig population

We recorded 412 fig trees of 12 species in the 25 sampled plots with more species recorded in the central parts of the reserve (Fig. 1). *Ficus lutea* (122 trees), *F. thonningii* (96), *F. abutilifolia* (78), *F. ovata* (39), *F. sycomorus* (19) were the most abundant species, with *F. platyphylla*, *F. ingens* and the unidentified species represented by one tree found each; the four other *Ficus* species found, at which we did not make frugivory observations, were *F. sur* (17 trees), *F. umbellata* (17), *F. glumosa* (13), *F. polita* (1). The overall density of the combined *Ficus* population in the reserve was 1.35 trees/ha.

### Visitation to *Ficus* spp.

We observed 3234 individual bird visits, representing 48 bird species visiting the 12 *Ficus* trees monitored (Table 1). *Ficus lutea* received the most bird species (38 species cumulatively for four individuals, which received 11, 17, 28 and 26 species each: mean species per tree = 20.5), followed by *F. abutilifolia* (19 species), *F. thonningii* and *F.* sp. (17 species each), *F. ingens* (15 species), *F. ovata* (14 species), *F. sycomorus* (18 species cumulatively for two individuals, which received 7 and 16 species each: mean species per tree = 11.5) and *F. platyphylla* (5 species).

More than half of the total number of bird visits (1665) were observed on the four trees of *F. lutea*, followed by *F. abutilifolia*, *F. ingens*, *F.* sp. and *F. sycomorus*, the three remaining species each receiving < 5% of visits (Table 2).

### Behaviour

The majority of bird visitors (> 55%) swallowed figs whole. We also observed birds perching and occasionally pecking out parts of the figs (29% of visits). The least frequent behaviour (5% of visits) consisted of birds (three species only, described as opportunistic frugivores and marked with asterisks in Table 1) eating insects rather than figs.

Several bird species visited multiple fig species (Table 1). Among the obligate frugivores, the Common Bulbul and the Yellow-fronted Tinkerbird were recorded on all eight *Ficus* species, and the Speckled Mousebird was recorded on seven of them. Opportunistic and partial frugivores were recorded in up to six species (Table 1).

The longest mean visit times were observed on *Ficus ingens*, followed by *F. ovata* and *F. sycomorus* (Table 2).

**Table 1. The total number of visits by each bird species to the eight *Ficus* species studied in Amurum Forest Reserve, Nigeria: *Fa*, *Fi*, *Fl*, *Fo*, *Fp*, *F*sp, *Fsy*, *Ft* correspond to *F. abutilifolia, F. ingens, F. lutea, F. ovata, F. platyphylla, F.* sp., *F. sycomorus* and *F. thonningii* respectively. The birds' frugivory category (see Methods) also indicates species that visited but ate only insects in the trees (marked *) and species that visited but did not eat figs or insects (*i.e.* perched without appearing to feed, marked †).**

| | Frugivory category | Visits to *Ficus* species | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | ***Fa*** | ***Fi*** | ***Fl*** | ***Fo*** | ***Fp*** | ***F*sp** | ***Fsy*** | ***Ft*** |
| **Scopidae** | | | | | | | | | |
| *Scopus umbretta* Hamerkop | opportunistic† | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| **Falconidae** | | | | | | | | | |
| *Falco biarmicus* Lanner Falcon | opportunistic† | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| **Columbidae** | | | | | | | | | |
| *Streptopelia hypopyrrha* Adamawa Turtle Dove | opportunistic | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *S. senegalensis* Laughing Dove | opportunistic | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *S. vinacea* Vinaceous Dove | opportunistic | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 |
| *Turtur abyssinicus* Black-billed Wood Dove | opportunistic | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| *Treron waalia* Bruce's Green Pigeon | obligate | 1 | 0 | 244 | 0 | 0 | 0 | 0 | 0 |
| **Musophagidae** | | | | | | | | | |
| *Musophaga violacea* Violet Turaco | obligate | 41 | 0 | 96 | 0 | 0 | 2 | 0 | 0 |
| *Crinifer piscator* Western Grey Plantain-eater | obligate | 32 | 0 | 95 | 2 | 0 | 0 | 17 | 1 |
| **Cuculidae** | | | | | | | | | |
| *Centropus senegalensis* Senegal Coucal | opportunistic | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| **Coliidae** | | | | | | | | | |
| *Colius striatus* Speckled Mousebird | obligate | 113 | 189 | 326 | 73 | 0 | 55 | 80 | 5 |
| **Meropidae** | | | | | | | | | |
| *Merops bulocki* Red-throated Bee-eater | opportunistic* | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| **Bucerotidae** | | | | | | | | | |
| *Tockus erythrorhynchus* Red-billed Hornbill | partial | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 1 |
| *T. nasutus* African Grey Hornbill | obligate | 4 | 1 | 157 | 0 | 0 | 19 | 9 | 1 |

| | Frugivory category | Visits to *Ficus* species | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | ***Fa*** | ***Fi*** | ***Fl*** | ***Fo*** | ***Fp*** | ***F*sp** | ***Fsy*** | ***Ft*** |
| **Lybiidae** | | | | | | | | | |
| *Pogoniulus chrysoconus* Yellow-fronted Tinkerbird | opportunistic | 4 | 1 | 3 | 1 | 2 | 1 | 2 | 1 |
| *Lybius dubius* Bearded Barbet | obligate | 8 | 4 | 179 | 0 | 0 | 1 | 33 | 23 |
| *L. vielloti* Vieillot's Barbet | partial | 0 | 0 | 57 | 0 | 0 | 10 | 0 | 7 |
| **Picidae** | | | | | | | | | |
| *Dendropicos fuscescens* Cardinal Woodpecker | opportunistic | 0 | 0 | 4 | 1 | 0 | 2 | 1 | 0 |
| *Mesopicos goertae* Grey Woodpecker | opportunistic | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| **Pycnonotidae** | | | | | | | | | |
| *Pycnonotus barbatus* Common Bulbul | obligate | 51 | 46 | 62 | 11 | 10 | 48 | 52 | 16 |
| *Chlorocichla flavicollis* Yellow-throated Leaflove | obligate | 1 | 4 | 49 | 0 | 0 | 0 | 0 | 4 |
| **Turdidae** | | | | | | | | | |
| *Turdus pelios* African Thrush | opportunistic | 45 | 4 | 41 | 13 | 0 | 12 | 20 | 0 |
| **Muscicapidae** | | | | | | | | | |
| *Myrmecocichla cinnamomeiventris* Mocking Chat | opportunistic | 11 | 1 | 6 | 0 | 0 | 23 | 0 | 0 |
| *Melaenormis edolioides* Northern Black Flycatcher | opportunistic | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| **Sylviidae** | | | | | | | | | |
| *Eremomela pusilla* Senegal Eremomela | opportunistic | 17 | 5 | 4 | 0 | 0 | 1 | 1 | 0 |
| *Sylvietta brachyura* Northern Crombec | opportunistic | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Phylloscopus trochilus* Willow Warbler | opportunistic | 0 | 1 | 7 | 0 | 0 | 0 | 0 | 0 |
| *Sylvia borin* Garden Warbler | opportunistic | 6 | 0 | 0 | 0 | 0 | 11 | 0 | 0 |
| *S. communis* Common Whitethroat | opportunistic | 1 | 25 | 18 | 2 | 0 | 1 | 13 | 0 |
| **Cisticolidae** | | | | | | | | | |
| *Camaroptera brachyura* Grey-backed Camaroptera | opportunistic | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 |
| *Prinia subflava* Tawny-flanked Prinia | opportunistic | 0 | 9 | 0 | 2 | 0 | 0 | 8 | 3 |
| **Platysteiridae** | | | | | | | | | |
| *Batis senegalensis* Senegal Batis | opportunistic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Monarchidae** | | | | | | | | | |
| *Elminia longicauda* Blue Flycatcher | opportunistic* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Terpsiphone viridis* Paradise Flycatcher | opportunistic* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| **Timaliidae** | | | | | | | | | |
| *Turdoides plebejus* Brown Babbler | opportunistic | 0 | 0 | 13 | 0 | 0 | 0 | 1 | 0 |
| **Remizidae** | | | | | | | | | |
| *Anthoscopus parvulus* Yellow Penduline Tit | opportunistic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| **Nectariniidae** | | | | | | | | | |
| *Chalcomitra senegalensis* Scarlet-chested Sunbird | opportunistic | 4 | 1 | 27 | 3 | 0 | 0 | 15 | 0 |
| *Nectarinia venusta* Variable Sunbird | opportunistic | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| **Zosteropidae** | | | | | | | | | |
| *Zosterops senegalensis* Yellow White-eye | partial | 0 | 4 | 12 | 2 | 0 | 6 | 22 | 4 |
| **Sturnidae** | | | | | | | | | |
| *Onychognathus morio* Neumann's Starling | obligate | 15 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Lamprotornis purpureus* Purple Glossy Starling | obligate | 0 | 0 | 183 | 0 | 1 | 40 | 61 | 0 |
| *Cinnyricinclus leucogaster* Violet-backed Starling | obligate | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 0 |
| **Passeridae** | | | | | | | | | |
| *Passer griseus* Grey-headed Sparrow | opportunistic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| **Ploceidae** | | | | | | | | | |
| *Ploceus heuglini* Heuglin's Masked Weaver | opportunistic | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *P. cucullatus* Village Weaver | opportunistic | 9 | 0 | 0 | 4 | 0 | 0 | 87 | 0 |
| **Estrildidae** | | | | | | | | | |
| *Estrilda caerulescens* Lavender Waxbill | opportunistic† | 31 | 0 | 24 | 1 | 9 | 3 | 1 | 0 |
| *Lagonosticta sanguinodorsalis* Rock Firefinch | opportunistic† | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *L. senegala* Red-billed Firefinch | opportunistic† | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| **Total visits** | | **395** | **296** | **1665** | **120** | **23** | **236** | **424** | **75** |
| **Number of species visiting** | | **19** | **15** | **38** | **14** | **5** | **17** | **18** | **17** |

**Table 2. Summary of *Ficus* species visited by birds during the study period. Fig sizes (mm) are reported as mean syconium length (first value) and width (second value). Habitat types: SW = savanna woodland; GF = gallery forest; RO = rocky outcrop.**

| *Ficus* species | Fig size in mm (n) | Habitat types | Total visits per tree | Time spent per visit (min.) | n figs eaten per visit |
|---|---|---|---|---|---|
| *abutilifolia* | 22.9 x 12.1 (44) | SW | 395 | 9.1 ± 10.9 | 3.9 ± 5.2 |
| *ingens* | 5.0 x 4.5 (30) | SW | 296 | 20.5 ± 19.2 | 4.8 ± 3.9 |
| *lutea* | 23.1 x 21.7 (80) | GF, SW | 416.25* | 12.2 ± 26.0 | 3.6 ± 5.5 |
| *ovata* | 27.5 x 28.8 (15) | RO | 120 | 15.5 ± 31.7 | 2.3 ± 1.7 |
| *platyphylla* | 14.0 x 13.1 (16) | RO | 23 | 2.9 ± 1.8 | 1.7 ± 1.1 |
| sp. indet. | 20.1 x 18.2 (30) | RO | 236 | 6.3 ± 5.6 | 3.9 ± 5.5 |
| *sycomorus* | 38.5 x 36.1 (23) | RO, SW | 212* | 15.2 ± 17.0 | 2.9 ± 2.4 |
| *thonningii* | 8.3 x 6.5 (40) | RO | 75 | 7.4 ± 5.8 | 5.2 ± 4.4 |

*Means of the visit numbers to the four *F. lutea* (826, 229, 302, 308 visits) and two *F. sycomorus* (29, 395 visits) trees observed: sample sizes for behavioural measures are the "total visits" column, except for *F. lutea* (n = 1665) and *F. sycomorus* (n = 424).

We found no strong correlation between mean number of figs consumed per visit and fig size (maximum dimension) ($r = –0.48$, $P = 0.23$, n = 8), although the two species with the smallest figs, *F. ingens* and *F. thonningii*, had the greatest mean number of figs eaten per visit (Table 2). There was also no significant correlation between the number of bird species that visited a tree and fig size, nor between total number of visits to a tree and fig size.

There was a general similarity in the daily pattern of use of the eight fig tree species by birds (Fig. 3), with most feeding activity occurring from 6h30 to 10h00 and the morning peak falling roughly between 8h00 and 9h30 (a little later in *F. platyphylla*). No visitors were seen on trees between noon and 13h00. There was a lesser period of activity from around 14h00 to 18h00, with its peak around 16h00 (Fig. 3).

The mean time spent per visit on each tree was similar among the four individuals of *Ficus lutea* (Tukey HSD test: $P > 0.05$; Fig. 4), but the numbers of visits by birds of different species and mean figs eaten per visit differed significantly between the four trees, in four and five of the six pairwise combinations, respectively (Tukey HSD tests, both $P < 0.05$; Fig. 4).

There was a strong correlation between mean length of visit and mean number of figs eaten per visit at each fig species ($r = 0.57$, $P < 0.001$, n = 8) and significant but weaker positive relationships between number of visits and mean number of figs eaten per visit ($r = 0.17$, $P < 0.001$, n = 8) and between number of visits and mean duration of the visit ($r = 0.12$, $P < 0.001$, n = 8).

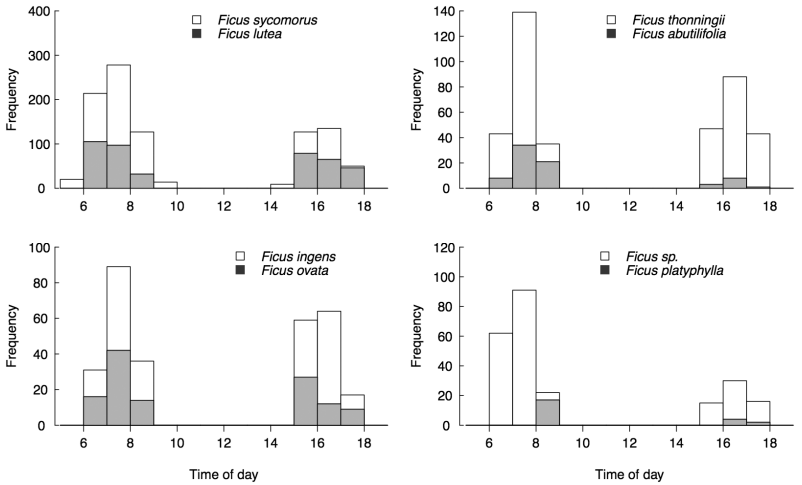


**Figure 3. Daily feeding patterns on eight *Ficus* species, as the frequency of bird visits for every hour of the day. Grey bars signify overlap between black and white.**

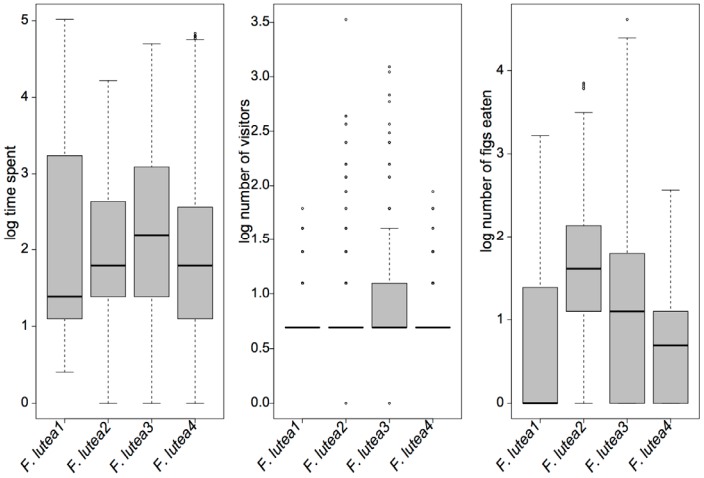


**Figure 4. Intra-specific differences in visitation pattern between individuals of *Ficus lutea*. The box ends mark the first and third quartiles, the median is indicated by the horizontal line, the range by the vertical dashed line, and outliers (points > 1.5 x the interquartile range) by circles. Data points on central graph are numbers of visitors of different bird species, whereas all species are grouped for visit times (left) and number of figs eaten (right).**

## Discussion

Differential attractiveness of *Ficus* species has previously been reported for African frugivores: for example, Bruce's Green Pigeon was said to favour *Ficus platyphylla* (Morel *et al*. 1986), although in the present study it was not noted on *F. platyphylla* but fed almost exclusively on *F. lutea*. Plant species that attract a diverse community of frugivores may similarly be important for frugivore survival (Peres 2000). The relationships observed in our study between birds and fig trees may reflect bird preferences for certain *Ficus* species. For example, *F. lutea* was the most visited fig species (per tree), in terms of both number of bird species and number of visits. The longest visit durations were on *F. ingens*, *F. ovata*, *F. sycomorus* and *F. lutea*, and the most fruits eaten per visit on *F. thonningii*, *F. ingens*, *F. abutilifolia* and *F*. sp., respectively. Of the three most abundant fig species in Amurum, *F. lutea*, *F. abutilifolia* and *F. thonningii*, the former two received the most visits per tree, whereas *F thonningii* received relatively few visits although its small fruits had the highest removal rate (mean figs removed per mean visit time) of all species (Table 2). The somewhat scarce *F. ingens* received many long visits but showed relatively low levels of fruit removal than more common species. Hence, the drivers of consumption are likely to be factors other than tree density.

Factors driving the usage of a particular fig species might include tree density, fruiting phenology, fig colour, fig nutritive value and fig size (Korine & Kalko 2000, Githiru *et al*. 2002, Herrera 2002, Bleher *et al*. 2003, Lord 2004). There was great variation in fig size between the eight *Ficus* species (Table 2; *cf.* Berg & Wiebes 1992), which could account for some of the variation in fig species attractiveness. But although species with small fruits are presumably accessible to a larger range of bird species, we found no significant relationships between fig size and visit frequency or number of bird species visiting.

For *F. lutea*, there were significant differences between the four trees in number of visitors and mean number of figs eaten per visit, although the numerical difference in the latter was slight. These intra-species differences indicate that the conclusions on interspecific differences below, based on only a single tree for most species, must be treated as preliminary.

There was a general similarity in temporal feeding patterns on all fig species, with heavy activity in the morning, except that activity on *F. platyphylla* occurred slightly later in the morning (but not in the afternoon) compared to other fig species. One possible reason could be that frugivores prefer the other species and later move onto *F. platyphylla* when the fruits that ripened overnight on the other species are depleted. Supporting this, *F. platyphylla* had a low number of birds visiting, and the lowest rate of fruit removal. As such, *F. platyphylla* may represent a "backup resource" relative to more preferred species. Choice tests could examine this possibility. The overall pattern of greatest visitation before 10h00 conforms to a common pattern of avian foraging and Breitwisch's (1983) finding at a *Ficus* in Cameroon.

Visitation in the morning was nearly three times higher to *F. thonningii* than to all other tree species, with a peak slightly later than all other trees except *F. platyphylla*; in the evening, the latter part of the afternoon peak in visitation to *F. thonningii* occurred when bird activities started declining on other fig trees (Fig. 3). *F. thonningii* appears to be an important food resource in Amurum; it is found at high density, and although visit times are relatively short, the heavy morning usage pattern and high fruit removal rates (with no figs dropped) suggest it is a preferred food for frugivorous birds. Bleher *et al*. (2003) found that *F. thonningii* provided the most reliable resources for birds in Oribi Gorge Nature Reserve in South Africa.

Our *Ficus* trees were utilized by some opportunistic frugivores which foraged for insects but were not seen to consume figs (Red-throated Bee-eater, Blue Flycatcher, Paradise Flycatcher). Additionally, a number of birds used focal trees for perching but not feeding at all, *e.g*. Hamerkop, Lanner Falcon, Lavender Waxbill, Red-billed Firefinch, and the Nigerian endemic Rock Firefinch.

Overall, our data on *Ficus*–bird associations show that figs are important resources for frugivorous birds in Amurum Forest Reserve. *Ficus lutea*, *F. ingens*, *F. thonningii* and *F. abutilifolia* in particular appear to be the most important fig resources for birds, though we remain cautious in this conclusion because our sample size was limited. The site harbours a high density of fig trees of a variety of species that are used by a large and diverse assemblage of visitors. Longer-term research should focus on the reproductive phenology as well as temporal and spatial availability of figs. This will help identify critical resources and potential keystone species that will inform conservation planning. Reforestation programs should not only consider species rarity and vulnerability but also give priority to plant species that are especially useful in sustaining bird diversity and ultimately ecosystem stability.

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