



Epauletted fruit bats prefer native plants and contribute to seed dispersal in a South African agricultural landscape

Vusani Mphethe^{1,2} | Sina Weier¹  | Catrin Westphal³  | Birthe Linden^{1,4,5} |
Lourens Swanepoel² | Daniel Parker^{6,7}  | Peter Taylor^{1,5}

¹SARChI Chair on Biodiversity Value and Change, Faculty of Science, Engineering and Agriculture, Thohoyandou, South Africa

²Department of Biological Sciences, Faculty of Science, Engineering and Agriculture, Thohoyandou, South Africa

³Functional Agrobiodiversity, Georg-August-University Göttingen, Göttingen, Germany

⁴Lajuma Research Centre, Louis Trichardt, Limpopo Province, South Africa

⁵Department of Zoology & Entomology & Afromontane Research Unit, University of the Free State, Phuthaditjhaba, South Africa

⁶School of Biology and Environmental Sciences, University of Mpumalanga, Mbombela, South Africa

⁷Wildlife and Reserve Management Research Group, Department of Zoology and Entomology, Rhodes University, Makhanda, South Africa

Correspondence

Sina Weier, SARChI Chair on Biodiversity Value and Change, Faculty of Science, Engineering and Agriculture, Thohoyandou, South Africa.
Email: sinaweier.univen@gmail.com

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: 405945293; National Research Foundation

Abstract

Fruit bats provide vital ecosystem services through seed dispersal aiding secondary forest regeneration. However, fruit bat species are often persecuted by fruit-growing farmers due to perceived and actual crop damage. In this study, we investigated the dietary components of *Epomophorous wahlbergi*, *Epomophorous crypturus* and *Rousettus aegyptiacus*, which are the three fruit bat species commonly found in litchi orchards and surrounding natural habitats in the Limpopo Province, South Africa. We further explored the contribution of fruit bats to seed dispersal and germination success. Fruit bat diet was dominated by wild fruit species (95%), while commercial fruit contributed little (2%) to their diet, even during the litchi harvest season. Fig seeds (*Ficus* spp.) collected from captured bats as spit outs had significantly lower germination rates than regular seeds, but a significantly lower germination latency. A similar pattern was observed for quinine trees (*Rauvolfia caffra*). Our results suggest that fruit bats inhabiting orchards and surrounding natural vegetation feed primarily on wild fruit trees, probably modulated by the high percentage of natural vegetation still found in our study area, supporting the importance of natural habitats in mitigating crop damage. We encourage further work on potential disservices by fruit bats and their habitat use.

KEYWORDS

agriculture, bat diet, habitat use, litchis, seed dispersal, seed germination

Résumé

Les chauves-souris frugivores fournissent des services écosystémiques vitaux en dispersant les graines et en favorisant la régénération des forêts secondaires. Cependant, les espèces de chauves-souris frugivores sont souvent persécutées par les exploitants de cultures fruitières en raison des dégâts perçus et réels causés aux cultures. Dans cette étude, nous avons analysé les composants alimentaires des *Epomophorous wahlbergi*, des *Epomophorous crypturus* et des *Rousettus aegyptiacus*, qui sont les trois espèces de chauves-souris frugivores communément trouvées dans les vergers de litchis et les habitats naturels environnants dans la Province de Limpopo,

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2023 The Authors. *African Journal of Ecology* published by John Wiley & Sons Ltd.

en Afrique du Sud. Nous avons également étudié la contribution des chauves-souris frugivores à la dispersion des graines et au succès de la germination. L'alimentation des chauves-souris frugivores était dominée par les espèces de fruits sauvages (95%), tandis que les fruits commerciaux contribuaient peu (2%) à leur alimentation, même pendant la saison de récolte des litchis. Les graines de figuier (*Ficus* spp.), recueillies sur ce que des chauves-souris en captivité ont recraché, présentaient des taux de germination considérablement plus faibles que les graines ordinaires, mais une latence de germination considérablement plus faible. Un schéma similaire a été observé pour les arbres à quinine (*Rauvolfia caffra*). Nos résultats suggèrent que les chauves-souris frugivores qui habitent les vergers et la végétation naturelle environnante se nourrissent principalement d'arbres fruitiers sauvages, probablement conditionnées par le pourcentage élevé de la végétation naturelle encore présent dans notre zone d'étude, ce qui confirme l'importance des habitats naturels dans l'atténuation des dégâts aux cultures. Nous encourageons la poursuite des travaux sur les dégâts potentiels des chauves-souris frugivores et leur utilisation de l'habitat.

1 | INTRODUCTION

Old World fruit bats (Pteropodidae) feed primarily on fruits, flowers (nectar, pollen) and leaves (Monadjem et al., 2020). Fruit bats have a plant-based diet (Aziz et al., 2021) that consists of a wide range of wild indigenous tree species (Bonaccorso et al., 2014; Monadjem et al., 2020; Seltzer et al., 2013). In the Philippines, the musky fruit bats (*Ptenochirus jagori*), Philippine pygmy fruit bats (*Haplonycteris fischeri*) and lesser musky fruit bats (*Ptenochirus minor*) often preferred *Ficus* spp. as their staple food (Relox et al., 2014). Similarly, Egyptian fruit bats in Cyprus were documented to feed on figs (*Ficus carica*) during the summer season (Lucan et al., 2016). In South Africa, Wahlberg's epauletted fruit bats were also reported to feed on fig species during foraging (Bonaccorso et al., 2014; Rollinson et al., 2013). Fruit bats may feed on commercial fruits, including mangoes (*Mangifera indica*), pawpaws (*Asimina triloba*), guavas (*Psidium guajava*), litchis (*Litchi chinensis*), bananas (*Musa acuminata*), dates (*Phoenix dactylifera*) and other exotic species such as syringa berries (*Melia azedarach*; Fleming et al., 2009). Raiding of commercial fruits by fruit bats can cause significant economic damage. For example, in Mauritius, Mauritian flying fox (*Pteropus niger*) and Rodrigues flying fox (*Pteropus rodricensis*) raiding backyard litchis and mango trees caused around 36%–42% of total damage (Price, 2013; Tollington et al., 2019). Similarly, Egyptian fruit bats in Egypt were reported to raid apple (*Malus pumila*), apricot (*Prunus armeniaca*), banana, custard apple (*Annona reticulata*), date, mandarin (*Citrus reticulata*), mango, mulberry (*Morus alba*), orange (*Citrus sinensis*), peach (*Prunus persica*), pear (*Pyrus communis* L.), plum (*Prunus domestica*), pomegranate (*Punica granatum*) and strawberry (*Fragaria ananassa*) orchards (Aziz et al., 2016). Such raiding of commercial fruits by fruit bats and associated losses can lead to human–wildlife conflict and subsequent persecution of fruit bats (Aziz et al., 2016; Fujita & Tuttle, 1991; Kunz et al., 2011). As such, it remains important to investigate factors leading to fruit-raiding behaviour and extent of damage. This is

especially important for Egyptian fruit bats which are perceived as potential crop raiders in commercial litchi farms in southern Africa (Jacobsen et al., 1986). Despite research showing that fruit bats can raid orchards, there is evidence that fruit bats prefer a natural diet. For example, captive Madagascan rousettes (*Rousettus madagascariensis*) preferred natural fruits to litchis as chemical composition analyses showed that lipid and calcium content were more important in fruit selection than fructose (Andrianaivoarivelo et al., 2012). This suggests that fruit bats might not pose a risk to commercial fruit production where fruits are picked/harvested unripe, as they prefer ripe fruit (Fleming et al., 2009; Monadjem et al., 2020). In Guinea, fruit bats target ripe mango orchards causing a significant damage to the fruits (Aziz et al., 2016; van Mele et al., 2009). However, in Australia, farmers adopted a practice of picking fruits such as bananas, mangoes and pawpaw unripe to avoid damage by flying foxes (*Pteropus* spp.), which avoid feeding on unripe fruits (Aziz et al., 2016). Previous studies on fruit raiding by fruit bats have also documented that bats feed on fruits that are too ripe to be sold on the market, and the damage to unripe fruits is a result of bats climbing over those fruit or due to test bites (Mickleburgh et al., 1992; van der Pijl, 1957).

In this study, we used three fruit bat species, Wahlberg's epauletted fruit bats (*Epomophorous wahlbergi*), Peters' epauletted fruit bats (*Epomophorous crypturus*) and Egyptian fruit bats (*Rousettus aegyptiacus*), to investigate fruit raiding behaviour in an agricultural matrix dominated by fruit orchards. Fruit bats are an ideal organism since they are potential fruit raiders, but the plant diet of fruit bats also results in important ecosystem services such as pollination and seed dispersal (Abedi-Lartey et al., 2016; Bonaccorso et al., 2014; Fahr et al., 2015; Fujita & Tuttle, 1991; Kunz et al., 2011). By consuming a variety of plant species, bats facilitate propagation of economically important plants, which produce fruits for drinks and food, ornamental plants, timber, dye, fibres, tannins, medicines and animal fodder (Fujita & Tuttle, 1991). Fruit bats (*Pteropodidae*) and flying foxes (*Pteropus*) in Africa and Australia can cover up to

1500km during migration, while foraging and dropping different varieties of seeds in flight (Richter & Cumming, 2008; Tidemann & Nelson, 2004). Similarly, telemetry work has shown Wahlberg's epauletted fruit bats travel over 13km between roosting and feeding sites in a single night, with individual bats visiting the same tree on more than one occasion (Bonaccorso et al., 2014). Radio-tracked Egyptian fruit bats flew 24km to forage in litchi orchards during litchi harvest season in Trichardtsdal, northern South Africa (Jacobsen et al., 1986). Fruit bats can enhance seed germination through mechanical and chemical scarification of the seed coat and the mixing of seeds with faecal materials, which has a fertilisation effect (Robertson et al., 2006; Rossaneis et al., 2015). Germinability of seeds after ingestion by bats can be viable and enhanced depending on bat and plant species interaction, with 95% of African tropical forests regenerated from seed droppings from fruit bats (BatCon, n.d.). Snode (2010) documented that sycamore fig (*Ficus sycamorus*) seeds passing through the gastrointestinal tract of Wahlberg's epauletted fruit bats have 88%–100% germination success in sterile Petri dishes.

Fruit bats provide important ecosystem services for forest regeneration, especially in deforested areas due to their ability to fly over a large distance across deforested areas (van Toor et al., 2019). Previous studies have reported that many plants visited by fruit bats have significant economic and health benefits to humans (Kunz et al., 2011; Scanlon et al., 2014). Fruit bats are known to disperse most plant species from *Ficus* (60 species), *Syzygium* (14 species) and *Diospyros* (8 species) genera (Aziz et al., 2021). Fig trees are important keystone species and food resources which sustain populations of frugivores that feed on their fruits including fruit bats (Bonaccorso et al., 2014; Pothasin et al., 2014). Similarly, *Syzygium* is also consumed by fruit bats (Monadjem et al., 2020), hence an important plant to cure diseases such as fever, malaria, tuberculosis, sexually transmitted infections (STIs) burns and gastrointestinal disorders (Maroyi, 2018). In Colombia, fruit bats were reported to facilitate ecosystem services of seed dispersion as well as increased soil fertility in agroecosystems (Enríquez-Acevedo et al., 2020). Fruit bats were documented to disperse approximately 20% of both widespread and endemic trees in the East Usambara Mountains of Tanzania (Seltzer et al., 2013). In Ghana, GPS-tracked straw-coloured fruit bats (*Eidolon helvum*) retained ingested seeds for a very long period while travelling large distances and potentially dispersing seeds up to a distance of 75.4 km (Abedi-Lartey et al., 2016).

Given the evidence of fruit raiding, as well as the potential for significant ecosystem services through seed dispersal, we aimed to determine the diet of fruit bats, their potential as seed dispersers as well as foraging behaviour in relation to ripe litchi fruits in commercial orchards. We hypothesised that litchis would predominate in the diet of fruit bats (Wahlberg's epauletted fruit bats, Peters' epauletted fruit bats and Egyptian fruit bats combined) in litchi orchards during the harvest season compared with samples from natural areas and those collected outside the harvest season. We predicted that seeds from spit outs might germinate more successfully (with a higher proportion of successful germination) with lower germination latency

(number of days taken to germinate) than regular seeds (Entwistle & Corp, 1997; Picot et al., 2007).

2 | MATERIALS AND METHODS

2.1 | Study area

2.1.1 | Kutetsha research camp (western Soutpansberg)

This study area was located within the Luvhondo Nature Reserve (−23.048014S; 29.447368E), at 1142m above sea level and is about 586ha in size (Figure 1) and is characterised by northern Mistbelt Forest, Soutpansberg Mountain Bushveld and Soutpansberg Summit Sourveld (Mucina & Rutherford, 2006). The Luvhondo Nature Reserve consists of several privately owned properties and is approximately 4300ha in size. Luvhondo Nature Reserve is situated on the Soutpansberg Mountain Range, a recognised centre of plant endemism (Hahn, 2017; van Wyk & Smith, 2001) and a centre of floristic diversity (Hahn, 2019). The Soutpansberg is further regarded as a hotspot for bat species (Cooper-Bohannon et al., 2016). The study site receives a mean annual rainfall of 724mm with a summer rainy season between December and February and a winter dry season between May and August (Ayers et al., 2020; Willems et al., 2009).

2.1.2 | Levubu (Farm Laatsgevonden) area (eastern Soutpansberg)

This study area was situated on Laatsgevonden Farm and surrounding farms in the Levubu area (−23.077443S; 30.338432E) located on the foothills of the Soutpansberg Mountain Range (636m above sea level), 18km west of Thohoyandou town in the north-eastern part of Limpopo Province (Figure 2). The size of the study area is about 647ha and characterised by a matrix of agricultural farms which cultivate avocados, bananas, guavas, litchis, macadamias (*Macadamia integrifolia*), mangoes, pineapples (*Ananas comosus*) and vegetables (Figure 2). Regarding cropping, the area is dominated by macadamias (128ha; 20%), followed by mangoes (44ha; 7%), bananas (43ha; 7%), guavas (15ha; 2%), litchis (13ha; 2%), avocados (7ha; 1%), vegetables (6ha; 1%) and pineapples (2ha; 0.4%), with the remaining percentage comprising abandoned guava, mango and banana plantation as well as roads, farmhouses, sheds, water ponds and the Lutanyanda river. The 13ha of litchis in the study area produces an annual litchi yield of about 5 tons. Around 94.26ha (15%) of the study area is characterised by natural vegetation, which includes wild fruit trees such as fig species, forest fever trees (*Anthocleista grandiflora*), water berries (*Syzygium cordatum*), quinine trees (*Rauvolfia caffra*), coastal golden-leaf (*Bridelia micrantha*) and alien exotics like syringa berries. The study area receives an annual summer rainfall of 1356mm during the wet summer season between the months of November and April (Tshililo et al., 2021).

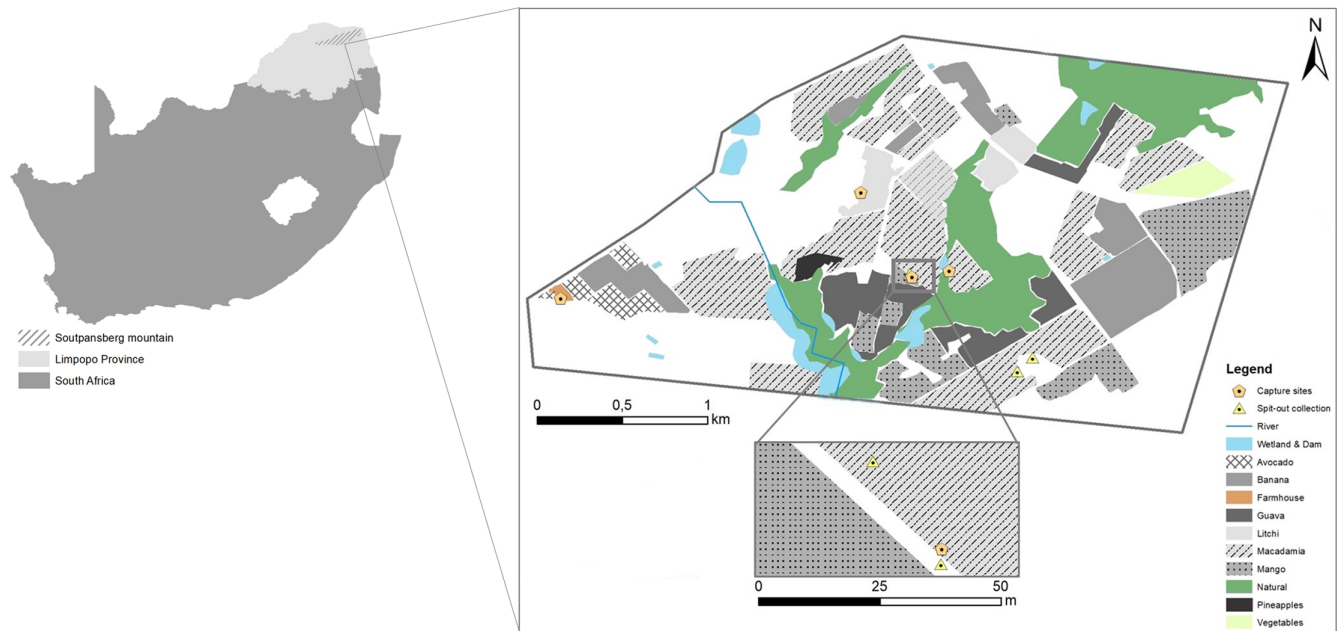


FIGURE 1 Map showing different land uses, localities of fruit bat captures and spit-out collection at Farm Laatsgevonden and the surrounding farms. The white patches are abandoned farms due to land claims, which were used to cultivate guava, mango, and banana fruits.

2.1.3 | Fruit bat capture and roost identification

Fruit bats were trapped in two study areas (Figures 1 and 2; Table 1) and during two study periods (litchi pre-ripe season and litchi ripe season) in the Soutpansberg mountain. Fruit bats were caught in litchi orchards (Figure 2) and in natural areas (Kutetsha Research Camp and Goro Game Reserve, Figure 1b). We caught fruit bats in litchi orchards during the litchi pre-ripe season in June (2019) as well as during the litchi ripe season in October (2019/2020), November (2019/2020) and December (2019/2020) in the vicinity of Laatsgevonden Farm in the Levubu sub-tropical agricultural area (eastern Soutpansberg). Natural habitats at the Kutetsha Research Camp and Goro Game Reserve (western Soutpansberg) were also sampled during litchi pre-ripe season (March (2019), June (2019) and September (2018)) and litchi ripe season (October (2018/2019), November (2018), January (2019) and February (2018)). Trapping was done between February 2018 and December 2020 in both litchi orchards and the natural area (Appendix S1). Fruit bats were trapped using mist nets (12 m, 9 m and 3 m) which were placed along pathways in natural habitats (Kutetsha Research Camp and Goro Nature Reserve) and litchi orchards (Figure 2). Nets were deployed at sunset and closed after 4 h during litchi pre-fruiting season (March–September) and 6 h in litchi harvest season (mid-October until end of February). Captured bats were identified in the field, following the identification key of Monadjem et al. (2020). Nets were checked every 5 min and captured bats were immediately placed in soft cotton bags for a maximum of 2–3 h allowing them to defecate in the bags so that faeces could be assessed for dietary components. Fruit bats

caught in mist nets were assessed for possible pulp on their body and mouth (e.g. litchi pulp), and distinctive odour/smell and colour of commercial fruits pulp such as guavas and litchis were determined (Voigt et al., 2009).

To determine fruit bats' diet, possible bat roosts and fruiting trees were identified (availability of spit outs on the ground) by visiting villages and farms in the Levubu area and asking locals about possible fruit bats evidence such as spit outs, roosts and foraging activity (Appendix S1).

The project was approved by the University of Venda Ethics Committee (Research Ethics Clearance Project Number: SMNS/19/ZOO/04/1909) for collection and handling of faecal materials.

2.1.4 | Fruit bat diet estimation

Dietary samples in the form of faeces, spit outs and dropped fruits were collected at 21 sites including feeding stations used by three species of fruit bats (Peters' epauletted fruit bats, Wahlberg's epauletted fruit bats and Egyptian fruit bats), and no Egyptian fruit bat roosts were found. Hence, spit outs collected from feeding roosts could not be assigned to a particular species but only to the genus (*Epomophorous*). Dietary samples collected from captured individuals had species identification (e.g. Wahlberg's epauletted fruit bats or Peters' epauletted fruit bats) (Table 2). Faecal matter and spit outs collected from the cloth bags of captured fruit bats were stored in glass vials for initial transportation and air-dried on plastic trays for 48 h. When dry, seeds from faeces and spit outs were sorted by colour and size and stored in plastic Ziplock bags to avoid



FIGURE 2 Map (a) shows the overall sampling sites of fruit bat captures and spit-out collection sites on both farming environment (Farm Laatsgevonden) and natural area (Kutetsha Research Camp), and (b) schematic outline of the Soutpansberg mountain range, fruit bat species distribution and *Rousettus aegyptiacus* cave roosts in the Soutpansberg mountain (1 = Kutetsha Research Camp in the Luvhondo Nature Reserve, 2 = Goro Game Reserve, 3 = Levubu Welgevonden area, 4 = Tshakhuma Mangwele caves and 5 = Levubu Laatsgevonden area).

TABLE 1 Capture success, trapping effort (trap nights) and number of captures for fruit bats in the western Soutpansberg (natural) as well as the eastern Soutpansberg (agricultural) of the Limpopo province.

| | Trap success (%) | Trap nights | <i>Rousettus aegyptiacus</i> | <i>Epomorphous crypturus</i> | <i>Epomorphous wahlbergi</i> |
|------------------------------|------------------|-------------|------------------------------|------------------------------|------------------------------|
| Agricultural Pre-ripe season | 0.71 | 7 | 0 | 5 | 0 |
| Agricultural Ripe season | 1.73 | 15 | 0 | 12 | 14 |
| Natural Pre-ripe season | 0.36 | 11 | 0 | 0 | 4 |
| Natural Ripe season | 1.08 | 13 | 4 | 0 | 10 |

development of mould, noting the date of collection, GPS coordinates and species name and sex. To collect spit outs, we searched for up to 30 min under each feeding station (fruiting tree) to collect fresh spit outs that could be found on the ground as well as on the leaves. Spit outs were dried in the same way as the faecal matter. Seeds were extracted from ripe fruits of potential food plants, dried and stored under the same conditions and later used in germination experiments. This collection was conducted during litchi pre-ripe season (March–April, June, July and September) as well as litchi ripe

season (October, November, December, January and February) in litchi orchards and natural areas. Faecal samples were examined after being rehydrated and sorted by using a sieve (sieve mesh diameter <1 mm) placed over a bucket. Spit outs collected from the ground were also rehydrated and sorted in the same manner as the faecal matter. Available seeds and fruit pulp were examined and, where possible, identified to genus or species level under a magnifying glass, using a reference seed library at the Lajuma Research Centre (Linden and Linden ongoing). The predominant component

TABLE 2 Total number of dietary samples collected, bat species and the type of samples collected during this study (seeds from faecal matter were not used in the germination experiments since very few seeds were collected from each sample).

| Bat species | Number of faecal matters | Number of spit outs | Total |
|------------------------------|--------------------------|---------------------|-------|
| <i>Epomophorus crypturus</i> | 12 | 2 | 14 |
| <i>Epomophorus wahlbergi</i> | 22 | 5 | 27 |
| Epauletted fruit bats | 1 | 20 | 21 |
| | | Total | 62 |

(seeds and pulp) of each sample was identified. Regular seeds and spit-out seeds were kept for a maximum of 6 days prior to sowing (Baskin & Baskin, 2014).

2.1.5 | Seed germination trial

Undamaged seeds from fruit bat spit outs were used in germination trials, with damaged seeds (seeds with small holes) excluded since they do not germinate (Steinbrechter & Leubner-Metzger, 2018). Seeds extracted from faecal samples were not used in the germination trials since the samples were too small for the experiment. Topsoil was used as the substrate and collected near trees of the same species as the planted seeds and fruits. The soil was first sieved with a sieve (mesh diameter <1 mm) to extract small stones, grass and other plant/weed seeds prior to the germination experiment.

Germination trials were conducted in a nursery covered with 30% shade cloth, in which germination trays were placed 1 m above ground level. We used one nursery, with seeds collected at the Lajuma Research Centre and Goro Game Reserve. Seed trays consisted of 200 cells, each measuring 27 × 27 mm with a drainage hole at the bottom. The same germination protocol was followed for the three treatment plant species of Figs (*Ficus* spp.), water berries (*Syzygium cordatum*) and quinine trees (*Rauvolfia caffra*) from which seeds were collected. Thus, seeds were planted in the same environmental conditions (light, water, temperature and humidity) except for the soil which was collected from specific sampling sites. Two treatments were used: seeds found in spit outs (masticated seeds) and regular seeds (manually extracted and cleaned seeds) (Naranjo et al., 2003). The soil samples used in both treatments were never sterilised in order to resemble seedling growth under natural conditions. Over one and a half trays (a total of 320 cells) were used for this experiment. The number of seeds planted in each cell depended on the size of the seed, thus seeds were planted so that they had at least 1.5 times the diameter of soil around them, and to push the seeds into the soil, the holes were dug 1.5 times deeper than the longest side of the seed (Baskin & Baskin, 2014).

Five fig spp. seeds were planted per cell/hole (Serio-Silva & Rico-Gray, 2002), two for water berries and one for quinine trees. The pots were monitored daily and watered whenever necessary when

the soil felt dry. In this trial, seed germination was considered by the appearance of a radicle, which is the first part of the seedling to emerge from the seed during the process of germination (Northam & Calliham, 1994). Seedlings were measured daily with a ruler, from the ground to the bottom of the top leaves. The germination experiment was set to 42 days (Davies et al., 2015) to ensure enough time for potential late germination. Treatments for water berries and an unidentified species were excluded from the analysis due to their spit outs completely failing to germinate.

2.1.6 | Fruit bat habitat use

A total of four fruit bats were collared with rechargeable MUSTELLA-60 GPS SRD collars, weighing a total of 6 g (Ecotone Telemetry, Slowackiego 12, 81-871 Sopot, Poland) during the 2019 and 2020 litchi seasons at Laatsgevonden Farm, Tshitwani Fruit farm and van Wyk farmhouse in the Levubu Laatsgevonden area. Loggers were programmed to take GPS positions every 5 min from 06:00 PM until 06:00 AM. To save power, the loggers automatically switched off while the bats were roosting during the day and later switched on, until the internal battery power was drained flat. An EP BS-P5 base station (Ecotone Telemetry, Slowackiego 12, 81-871 Sopot, Poland) with an omnidirectional antenna was used to remotely download data from the GPS logger on the collared animals at a range between 30 and 50 m. The base station was mounted on a 3 m flagpole above the ground in an area where the collared bats were caught for the whole night at farm Laatsgevonden and van Wyk farmhouse. However, to avoid theft, the base station was deployed until 2:00 am at Tshitwani fruit farm. Drive transects were also conducted in search of the collared bats, with an omnidirectional antenna mounted on the roof of a vehicle around litchi orchards and a 5 km radius distance from fruit bat capture site. From the four collared bats, one female Wahlberg's epauletted fruit bat was detected by our base station on the fourth night after the night of capture and here, the collar produced a total of 48 GPS fixes. Thereafter, she was never detected again nor could we recover the GPS logger despite an extensive ground search (Appendices S3 and S5). However, the logger produced five nights of GPS data and an average of 9.6 points per night. Of the three Peters' epauletted fruit bats, one was detected by the base station, but no GPS fixes were recovered, with the logger reporting a possible malfunction (error message NO SAT), and despite extensive search, the loggers were never recovered, nor the collared bats captured again.

2.1.7 | Data analysis – Diet and seed germination

The iNEXT (iNterpolation and EXTrapolation) package for R was used to determine sample completeness of dietary samples collected during pre-ripe litchi season and ripe litchi season in litchi orchards (farm) and natural areas (Chao & Chiu, 2016). This package computes the estimated diversities for standardised samples with common sample size and sample completeness and compares their diversity estimates

based on the seamless rarefaction and extrapolation sampling curves of Hill numbers of order q , species richness ($q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$; Colwell et al., 2012). We used the incidence data (reference sample) to compute diversity estimates, and the associated 95% confidence intervals were obtained by a bootstrap method and plotted the sample-size-based R/E sampling curves (plots diversity estimates with respect to sample size) and the coverage-based R/E sampling curves (plots diversity estimates with respect to sample coverage). The estimated sample completeness ($q = 0$) for farm pre-ripe litchi season: the data cover at most 92.31% of the total species in the assemblage (Appendix S4) and 87.52% during ripe litchi season (Chao et al., 2020). However, the estimated sample completeness for natural area: the data covered 100% of the total species in the assemblage during litchi pre-ripe and ripe season (Appendix S4).

We used generalised linear mixed-effects models (GLMMs) to investigate the effect of fruit bat seed spat outs on the probability of germination (binomial) and germination latency (Gaussian) in fig spp. (Crawley, 2007). GLMMs are the preferred model of analysis for germination data (Sileshi, 2012) since it allows for nested designs, non-normal distributions of the response variable as well as random-effect specification (Bolker et al., 2009; Sileshi, 2012). We modelled seed treatment (RS = regular seed and SO = spit out) as the fixed effects to evaluate the effect of fruit bats consuming seeds on the probability of germination and germination latency. We contrasted the 'treatment' model to a null model (no effect modelled) and evaluated model parsimony with Akaike information criteria (Symonds & Moussalli, 2010) and likelihood ratio tests (Lewis et al., 2011). GLMMs were fitted in R version 3.5.1. (R Core Team, 2018) using the lme4 package (Bates et al., 2015). Since there was not enough data to run the GLMM model for quinine trees, we used a non-parametric Kruskal-Wallis test (Crawley, 2007) to test for the difference in sample group mean of plant species treatment (regular seeds and spit-out seeds) for this species. The Kruskal-Wallis test was conducted in R 3.5.2 (R Development Core Team, Vienna, available at <http://www.r-project.org>, accessed 2021). Statistical tests were conducted between treatments and day of germination, and height at cut-off day (day 30).

3 | RESULTS

3.1 | Trapping and species

A total of 49 fruit bats were caught during 46 nights of sampling, of which 24 nights were sampled in natural habitats and 22 nights in litchi orchards. Seventeen Peters' epauletted fruit bats and 28 Wahlberg's epauletted fruit bats were caught. Only four Egyptian fruit bats were caught in the mist nets, and could not yield any spit outs and faecal matter, nor any active cave roost was found during our study period. As a result, this species could not provide any seeds to be used for germination trials (Appendix S2). The known Egyptian fruit bats cave roost (Mangwele cave) in Tshakhuma was vandalised by church people and shows no sign of fruit bats every time we visited during the course of this study. Five fruit bats were caught during litchi pre-ripe

season and 26 during ripe litchi season in litchi orchards in Levubu. Three fruit bats were caught in natural areas during pre-ripe litchi season and 15 were caught during the litchi ripe season.

3.2 | Fruit bat diet

We identified six species of wild indigenous fruits and one alien exotic fruit species in the diet of fruit bats during our study (Figure 3). Fruit bat diet revealed that bats fed mostly on wild *Ficus* spp., forest fever trees and alien exotic fruits of the syringa berry trees (Figure 3). Dietary composition showed that bats fed mostly on wild *Ficus* spp. and forest fever trees during ripe litchi season (Figure 3a). However, we found evidence of spit outs of *Ficus* spp., alien exotic fruits of syringa berries and guavas in the vicinity of litchi orchards in Levubu during pre-ripe litchi season. Moreover, dietary assessment revealed that fig spp., syringa berries, forest fever trees and coastal golden leaves dominated the bat diet in litchi orchards (Figure 3b).

3.3 | Probability and latency of germination

A total of 500 *Ficus* spp. seeds were planted, 250 (50%) for spit outs ('SO') and 250 (50%) for regular seed ('RS') treatments. For quinine trees, 80 seeds were planted (40 for 'SO' and 40 for 'RS').

Germination probability was higher in RS versus SO for both fig species and quinine tree (Figure 4). *Ficus* spp. have shown germination success of 18% for RS and 10% for SO, and quinine trees, 50% for RS and 28% for SO (Figure 4).

For *Ficus* spp., the treatment model had more support (AIC = 388.129) than the NULL model (AIC = 399.033), where SO seeds had a significantly lower ($df = 1$, $x^2 = 12.905$, $p < 0.001$) germination probability than SR (Figure 5a). For *Ficus* spp., for the germination latency, the treatment model had slightly more support (AIC = 457.230) than the NULL model (AIC = 459.604), where SO seeds had a significantly lower ($df = 1$, $x^2 = 4.373$, $p = 0.036$) germination latency than RS (Figure 5b).

For quinine trees, there was no significant difference in germination latency between treatments (SO and RS) ($df = 1$, $x^2 = 0.274$, $p = 0.601$), with mean rank of 17.14 (SE = 3.19) for SO and 15.37 (SE = 1.82) for RS. Quinine trees also showed no statistically significant difference between treatments in the height at cut-off day (day 30) ($df = 1$, $x^2 = 0.1881$, $p = 0.664$) with mean rank of 16.91 (SE = 2.97) for SO and 15.500 (SE = 1.82) for RS.

3.4 | Fruit bat habitat use

Although the data were not enough for us to conclude that the collared bats did not use litchi orchards while foraging, results from a single GPS-tracked female Wahlberg's epauletted fruit bat collared during ripe litchi season in Levubu demonstrated that the bat foraged near its roost without flying large distance during ripe litchi

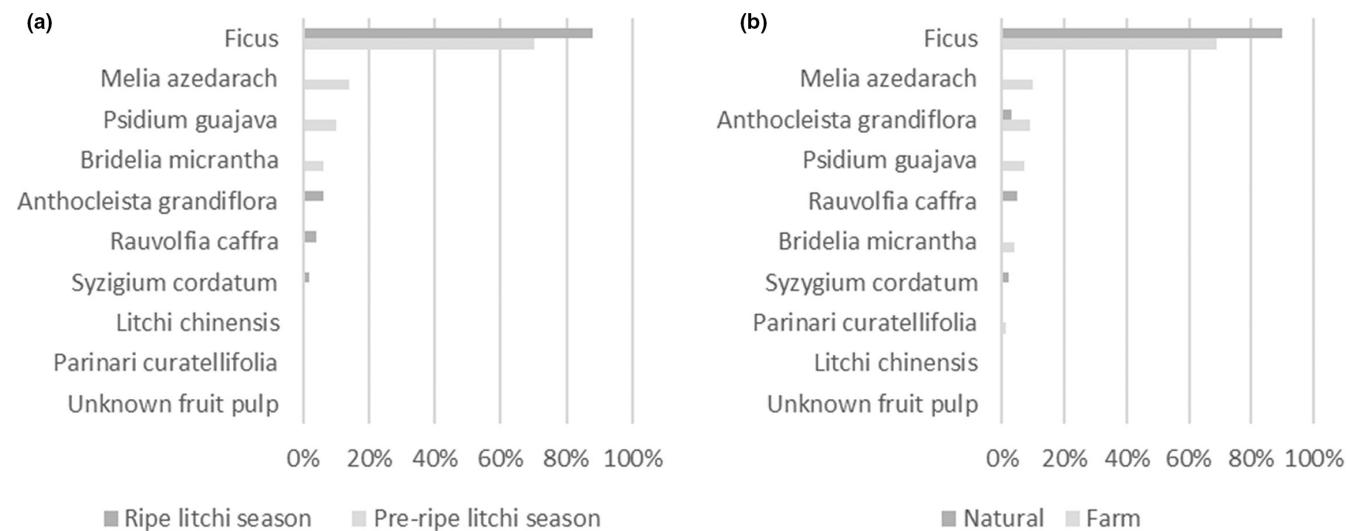


FIGURE 3 Diet of fruit bats expressed as percentage of faecal samples and spit outs containing fruit seeds and pulp collected from faeces, mouth and as spit outs of *Epomophorous* spp. (*crypturus* and *wahlbergi* combined) during (a) the two litchi seasons (dark grey colour – ripe litchi (harvest) season; light grey colour – pre-ripe litchi season) and (b) two study areas (dark grey colour – fruits consumed by fruit bats in natural area; light grey colour – fruits consumed by fruit bats on farming area).

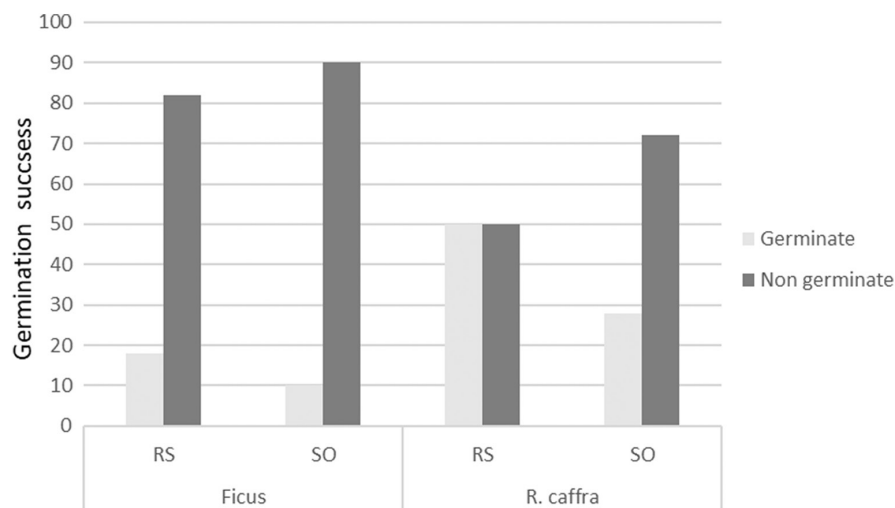


FIGURE 4 Germination success between treatment (RS, regular seeds; SO, spit out seeds) of *Ficus* spp. and *Rauvolfia caffra* for epauletted fruit bats (*E. wahlbergi* and *E. crypturus*). Germination success was measured as total number of germinated seeds (seeds that managed to sprout during germination trial) of either SO or RS divided by total number of SO or RS, multiplied by 100.

season and did not include/fly over ripe litchi situated about 250m away (Appendix S5). The collared bat spent much of its time foraging along the natural habitat on the edge of macadamia orchards of which several wild fruit species such as *Ficus* spp., water berries, quinine trees, mobola plums, forest fever trees and alien exotic fruit species such as syringa berries and guavas were identified by direct observation (Appendix S5). *Ficus* spp., quinine trees and forest fever trees were fruiting during bat collaring time.

4 | DISCUSSION

4.1 | Diet

Our dietary assessment indicated that in both natural and agricultural (litchi orchards) habitats and both the litchi ripe and pre-ripe seasons, epauletted fruit bats (*Epomophorous* spp.) fed

mostly on wild fruit species such as *Ficus* spp., forest fever trees, coastal golden leaves, mobola plums, quinine trees and water berries. Previous studies supported this finding in that epauletted fruit bats show a preference for wild fruits and, particularly, figs (Arumogum et al., 2019; Bonaccorso et al., 2014; Monadjem et al., 2020). Wahlberg's epauletted fruit bats have been documented to feed on *Ficus* spp. in KwaZulu Natal, South Africa (Rollinson et al., 2013; Raji & Downs, 2021). Seed dispersal by fruit bats is very important to the ecosystem and helps with plant communities' maintenance and forest regeneration (Bortolamiol et al., 2014; van Toor et al., 2019). A recent study (Aziz et al., 2021) revealed that fruit bats dispersed most of the seeds from the *Ficus* spp. genus. Epauletted fruit bats in our study areas could facilitate dispersion of a keystone species (*Ficus* spp.) which is also an important natural food resource for bats and other frugivores species (Pothasin et al., 2014). Previous studies (Adams & Snode, 2013; Bonaccorso et al., 2014) conducted in the Kruger National Park

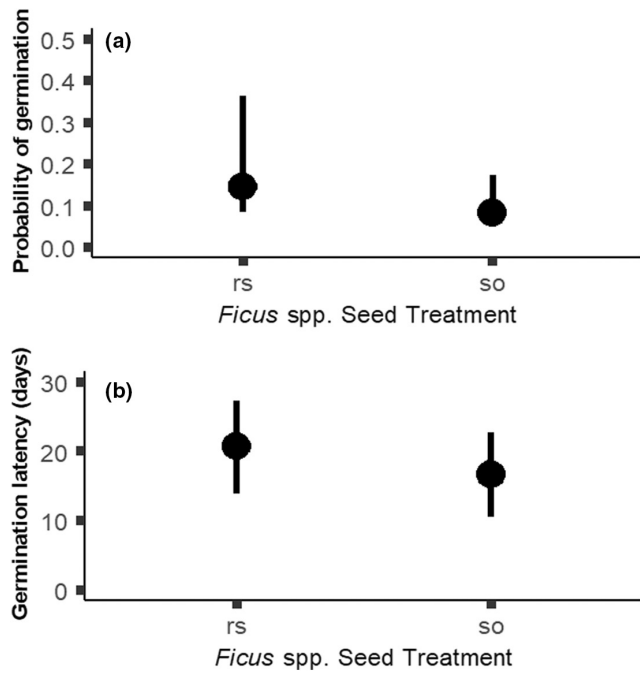


FIGURE 5 (a) Probability of germination (measured as the chances of seed to germinate) of bat-dispersed fruit species' seeds subject to different processing treatments (RS, regular seeds; SO, spit out seeds), and (b) germination latency (measured as the time taken by first seed to germinate from the sowing of all the seeds of SO and RS) of bat-dispersed fruit species' seeds subject to different processing treatments (RS, regular seeds; SO, spit out seeds).

documented that epauletted fruit bats prefer to feed on large quantities of ripe figs which pass through their gastrointestinal tracts undamaged and enhanced after being transported large distances from the feeding sites.

In contradiction to our findings for epauletted fruit bats, Egyptian fruit bats were reported to target litchi orchards during the ripe litchi season in South Africa and Mauritius (Fleming et al., 2009; Jacobsen & du Plessis, 1976; Tollington et al., 2019). Epauletted fruit bats did not seem to use ripe litchi orchards for foraging in our study, which could be because of their preference for wild fruits such as sycamore figs (Bonaccorso et al., 2014) and the availability of wild fruiting trees in natural habitat patches. At the finest scale of this study in the vicinity of Laatsgevonden Farm in the Levubu area, riparian natural habitats were available in the agricultural matrix dominated by fruit orchards and our data from a single-tracked female Wahlberg's epauletted fruit bats demonstrated the almost exclusive use of the riparian habitat by this individual in preference over nearby orchards which included litchi orchards with ripe fruit at the time. However, one cannot conclude that the tracked bat did not use the litchi orchards since the logger missed 90% of the points/GPS fixes it was supposed to collect. The Levubu agricultural area is situated on the foothills of the Soutpansberg Mountains, the upper slopes of which retain considerable areas of natural vegetation where wild fruiting trees could be available to foraging fruit bats resident in the Levubu area.

4.2 | Seed germination

Seed germination trials (RS and SO) demonstrated no positive effects of fruit bats on seedling germination for both *Ficus* spp. and quinine trees (Figure 4). These results conflict with findings by previous studies on epauletted fruit bats (Peters' epauletted fruit bats and Wahlberg's epauletted fruit bats) on seed germination of sycamore figs which reported that seeds from SO tend to germinate more successfully than RS (Snoder, 2010; Andrianaivoarivelo et al., 2011; de Carvalho-Ricardo et al., 2014). Our study showed that fewer *Ficus* spp. SO seeds germinated compared to RS. This is in contrast to previous studies which documented 88%–100% germination success (Snoder, 2010). Our study also demonstrated that although fewer numbers of *Ficus* spp. SO managed to germinate, their germination latency was improved compared to the RS, with SO germinating sooner than RS. These results are similar to findings by Andrianaivoarivelo et al. (2011), who documented that rubber fig (*Ficus rubra*) seeds germinated faster than RS after they had been ingested by Madagascar rousettes. Given their potential to disperse large number of *Ficus* spp. seeds as SO and improve their germination latency, epauletted fruit bats could help in habitat restoration of degraded landscapes. Our study confirms that fruit bats in our study area provide important ecosystem service of seed dispersal of keystone natural food source (*Ficus* spp.) and provides strong evidence for promoting their conservation, especially in agricultural settings where they are under threat due to perceived damage by commercial litchi farmers. Our study also showed no effect of treatment (RS and SO) on day of germination as well as on height on cut-off day for quinine trees. Other studies have documented higher germination success as well as shorter germination latency for seeds ingested by fruit bats (Andrianaivoarivelo et al., 2011; de Carvalho-Ricardo et al., 2014). Our sample size was small, and this could also explain the lower germination success results compared to previous studies (Andrianaivoarivelo et al., 2011; de Carvalho-Ricardo et al., 2014; Snoder, 2010). We suggest that future studies improve the germination trial/treatment design, and include planting of entire fruit, effect of pulp removal, pulp removal plus mechanical scarification of the seed coat, pulp removal plus mechanical and chemical scarification and gut passage effect plus fertiliser effect from faecal matter. Increased sampling effort in terms of bat captures as well as feeding experiments (feeding of ripe fruits under study to captured bats) could also account for an improved sample size.

4.3 | Habitat use

Our tagged female Wahlberg's epauletted fruit bats spent most of its time foraging over natural habitats and did not include litchi orchards during the litchi harvest season (Appendix S5). This result contrasts with those of previous studies which documented that fruit bats (such as Egyptian rousettes and Mauritius fruit bats) raid litchi orchards during litchi harvest season (Jacobsen et al., 1986; Jacobsen & du Plessis, 1976; Tollington et al., 2019). Similarly, fruit

bats were perceived to raid litchi orchards in Pakistan, resulting in the contamination and damage of fruits (Ali et al., 2022). The tracked Wahlberg's epauletted fruit bats spent most of its time foraging very close to its roost, concentrating its activity over natural habitats with ripe figs. These findings are similar to those of a previous study where Wahlberg's epauletted fruit bats concentrated its activity within 400m of a ripe sycamore fig tree (Bonaccorso et al., 2014). Dietary assessment of Pteropodid bats in Madagascar revealed that these species fed on large quantities of *Ficus* seeds over ripe litchi fruits (Raharimihaja et al., 2016). The ability of a tagged Wahlberg's epauletted fruit bat to feed on ripe *Ficus* spp., especially during litchi harvest season, provides enough evidence that fruit bats in Levubu do not target litchi orchards, and could be potential providers of an ecosystem service of seed dispersal of native *Ficus* spp. and help facilitate habitat restoration. Our study also provides enough evidence that a need for the conservation of these species (epauletted fruit bats) is crucial for the maintenance of indigenous plant community (*Ficus* spp.).

5 | CONCLUSION

Our dietary assessment as well as camera trapping surveys (Mphethe, unpublished) provide enough evidence that the two epauletted fruit bat species (*Epomophorous*) in Levubu do not raid litchi orchards. Perhaps, there is a difference among dietary needs of *Epomophorous* (in Levubu), *Rousettus* (Jacobsen et al., 1986) and *Pteropus* (Tollington et al., 2019) or it could be that colonial genera like *Rousettus* and *Pteropus* that feed in groups may be more able to safely exploit these orchards compared to *Epomophorous* which do not seem to feed in groups and only roosts in small groups (Monadjem et al., 2020). Moreover, our results could indicate that epauletted fruit bats prefer wild fruit over cultivated fruits (Andrianaivoarivelo et al., 2012).

The GPS tracking technique we used was relatively unsuccessful in our study, largely due to the unfavourable terrain and presence of many fences in the farming landscape which made it difficult to access a wide range of sites. The method would have worked better if we had managed to locate a stable large cave roost of the colonial Egyptian fruit bats. Anecdotal records suggest that a roost of this species occurred at Mangwele cave in Tshakhuma (Appendix S5). However, based on communication with local residents, this cave was vandalised by people and is no longer occupied (Mphethe, personal observation). Moreover, few individuals of epauletted fruit bats caught weighed <100g, which is the minimum weight allowed to fit the GPS transmitter humanely, hence it would have been easier to tag 10 individuals of Egyptian fruit bats which are slightly larger than epauletted fruit bats if it had been recorded in the area. Previous studies using radio tracking rather than GPS tracking (Bonaccorso et al., 2014; Rollinson et al., 2013) have produced good results on epauletted fruit bats foraging ecology, thus future studies on this species in a similar setup should consider using radio tracking.

We recommend that it is vital to educate farmers on the ecological benefits of having fruit bats around their orchard habitats, hence the importance of protecting natural areas around their farms. Public awareness can help in addressing the problem of human-wildlife conflict and play an important role in species conservation (Nyhus, 2016).

ACKNOWLEDGEMENTS

The study was funded by National Research Foundation (NRF) under the South African Research Chair on Biodiversity Value and Change in the Vhembe Biosphere Reserve. We are grateful to the South African Litchi Grower Association, SALGA (particularly Fritz Ahrens, Dennis Gilbert, Mandy Hugo, Shandukani Mulaudzi and Herman de Jager for allowing us to use their property as our study sites, and to many other litchi farmers who have shown keen interest in bats and offered support for this project). We are grateful to Jabu Linden who helped a lot in seed identification, not forgetting Claire Anne (Intern at Kutetsha Research Camp who collected much of the data in this manuscript). C.W. is grateful for funding from the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – Project number 405945293.

CONFLICT OF INTEREST STATEMENT

None to declare.

DATA AVAILABILITY STATEMENT

All data collected for this study and not included in the manuscript or its Appendices can be requested from the corresponding author and will be made available freely.

ORCID

Sina Weier  <https://orcid.org/0000-0003-3922-1495>

Catrin Westphal  <https://orcid.org/0000-0002-2615-1339>

Daniel Parker  <https://orcid.org/0000-0001-7555-5674>

REFERENCES

- Abedi-Lartey, M., Dechmann, D. K. N., Wikelski, M., Scharf, A. K., & Fahr, J. (2016). Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. *Global Ecology and Conservation*, 7, 12–24. <https://doi.org/10.1016/j.gecco.2016.03.005>
- Adams, R. A., & Snode, E. R. (2013). Unique insights into dispersion distances among calling males of Wahlberg's Epauletted fruit bat in Kruger National Park, South Africa. *The Open Ecology Journal*, 6, 54–60. <https://doi.org/10.2174/1874213001306010054>
- Ali, S., Javid, A., Imran, M., Khan, T. M., Phelps, K., & Olival, K. J. (2022). Knowledge, perceptions, and attitudes by residents in Punjab and Khyber Pakhtunkhwa, Pakistan in connection with bats. *Journal of Ethnobiology and Ethnomedicine*, 18(1), 43. <https://doi.org/10.1186/s13002-022-00541-9>
- Andrianaivoarivelo, R. A., Jenkins, R. K. B., Petit, E. J., Ramilijaona, O. R., Razafindrakoto, N., & Racey, P. A. (2012). *Rousettus madagascariensis* (Chiroptera: Pteropodidae) shows a preference for native and commercially unimportant fruits. *Endangered Species Research*, 19, 19–27. <https://doi.org/10.3354/esr00441>
- Andrianaivoarivelo, R. A., Ramilijaona, O. R., Racey, P. A., Razafindrakoto, N., & Jenkins, R. K. B. (2011). Feeding ecology, habitat use and reproduction of *Rousettus madagascariensis* Grandidier, 1928

- (Chiroptera: Pteropodidae) in eastern Madagascar. *Mammalia*, 75, 69–78. <https://doi.org/10.1515/mamm.2010.071>
- Arumooogum, N., Schoeman, M. C., & Ramdhani, S. (2019). The relative influence of abiotic and biotic factors on suitable habitat of Old World fruit bats under current and future climate scenarios. *Mammalian Biology*, 98, 188–200. <https://doi.org/10.1016/j.mambio.2019.09.006>
- Ayers, A. M., Allan, A. T. L., Howlett, C., Tordiffe, A. S. W., Williams, K. S., Williams, S. T., & Hill, R. A. (2020). Illuminating movement? Nocturnal activity patterns in chacma baboons. *Journal of Zoology*, 310(4), 287–297. <https://doi.org/10.1111/jzo.12747>
- Aziz, S. A., Mcconkey, K. R., Tanalgo, K., Sritongchuy, T., Low, M.-R., Yong, J. Y., Mildenstein, T. L., Nuevo-Diego, C. E., Lim, V. C., & Racey, P. A. (2021). The critical importance of old world fruit bats for healthy ecosystems and economies. *Frontiers in Ecology and Evolution*, 9, 377–426. <https://doi.org/10.3389/fevo.2021.641411>
- Aziz, S. A., Olival, K. J., Bumrungsri, S., Richards, G. C., & Racey, P. A. (2016). The conflict between pteropodid bats and fruit growers: Species, legislation and mitigation. In *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 377–426). Springer. https://doi.org/10.1007/978-3-319-25220-9_13
- Baskin, C. C., & Baskin, J. M. (2014). Ecologically meaningful germination studies. In *Seeds - ecology, biogeography, and evolution of dormancy and germination* (2nd ed., pp. 5–35). Academic Press.
- Batcon. (n.d.). In *Bat Conservation International*. Retrieved from <https://www.batcon.org>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *The Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Henry, M., Stevens, H., White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Bonaccorso, F. J., Winkelmann, J. R., Todd, C. M., & Miles, A. C. (2014). Foraging movements of epauletted fruit bats (Pteropodidae) in relation to the distribution of sycamore figs (Moraceae) in Kruger National Park, South Africa. *Acta Chiropterologica*, 16, 41–52. <https://doi.org/10.3161/150811014X683255>
- Bortolamiol, S., Cohen, M., Potts, K., Pennec, F., Rwaburindore, P., Kasenene, J., Seguya, A., Vignaud, Q., & Krief, S. (2014). Suitable habitats for endangered frugivorous mammals: Small-scale comparison, regeneration forest and chimpanzee density in Kibale National Park, Uganda. *PLoS ONE*, 9(7), e102177. <https://doi.org/10.1371/journal.pone.0102177>
- Chao, A., & Chiu, C.-H. (2016). Bridging two major approaches (the variance framework and diversity decomposition) to beta diversity and related similarity and differentiation measures. *Methods in Ecology and Evolution*, 7, 919–928. <https://doi.org/10.1111/2041-210X.12551>
- Chao, A., Kubota, Y., Zeleny, D., Chiu, C.-H., Li, C.-F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C.-L., Costello, M. J., & Colwell, R. K. (2020). Quantifying sample completeness and comparing diversities among assemblages. *Ecological Research*, 35, 292–314. <https://doi.org/10.1111/1440-1703.12102>
- Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S. Y., Mao, C. X., Chazdon, R. L., & Longino, J. T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblage. *Journal of Plant Ecology*, 5, 3–21. <https://doi.org/10.1093/jpe/rtr044>
- Cooper-Bohannon, R., Rebelo, H., Jones, G., Cotterill, F., Monadjem, A., Schoeman, C., Taylor, P. J., & Park, K. (2016). Predicting bat distributions and diversity hotspots in southern Africa. *Hystrix*, 27. <https://doi.org/10.4404/hystrix-27.1-11722>
- Crawley, M. J. (2007). *The R book* (Vol. 13, 978-0-470-51024-7). Wiley. <https://doi.org/10.1007/s00362-008-0118-3>
- Davies, R., di Sacco, A., & Newton, R. (2015). *Germination testing: Procedures and evaluation. Technical information sheet.*
- de Carvalho-Ricardo, M. C., Uieda, W., Fonsela, R. C. B., & Rossi, M. N. (2014). Frugivory and the effects of ingestion by bats on the seed germination of three pioneering plants. *Acta Oecologica*, 55, 51–57.
- Enríquez-Acevedo, T., Pérez-Torres, J., Ruiz-Agudelo, C., & Suarez, A. (2020). Seed dispersal by fruit bats in Colombia generates ecosystem services. *Agronomy for Sustainable Development*, 40(45). <https://doi.org/10.1007/s13593-020-00645-0>
- Entwistle, A. C., & Corp, N. (1997). The diet of Pteropus voeltzkowi, and endangered fruit bat endemic to Pemba Island, Tanzania. *African Journal of Ecology*, 35, 351–360.
- Fahr, I., Abedi-Lartey, M., Esch, T., Machwitz, M., Suu-Ire, R., Wikelski, M., & Dechmann, D. K. N. (2015). Pronounced seasonal changes in the movement ecology of a highly gregarious central-place forager, the African straw-coloured fruit bat (*Eidolon helvum*). *PLoS One*, 10, e0138985. <https://doi.org/10.1371/journal.pone.0138985>
- Fleming, T. H., Geiselman, C., & Kress, W. J. (2009). The evolution of bat pollination - A phylogenetic perspective. *Annals of Botany*, 104, 1017–1043. <https://doi.org/10.1093/aob/mcp197>
- Fujita, M. S., & Tuttle, M. D. (1991). Flying foxes (Chiroptera: Pteropodidae): Threatened animals of key ecological and economic importance. *Conservation Biology*, 5, 455–463.
- Hahn, N. (2017). Endemic flora of the Soutpansberg, Blouberg and Makgabeng. *South African Journal of Botany*, 113, 324–336. <https://doi.org/10.1016/j.sajb.2017.09.006>
- Hahn, N. (2019). Indigenous vascular plants of the Soutpansberg, South Africa. *Bothalia - African Biodiversity and Conservation*, 49, 1–5. <https://doi.org/10.4102/abc.v49i1.2402>
- Jacobsen, N. H. G., & du Plessis, E. (1976). Observations on the ecology and biology of the cape fruit bat *Rousettus aegyptiacus leachi* in the eastern Transvaal. *South African Journal Science*, 72, 270–273.
- Jacobsen, N. H. G., Viljoen, P. C., & Ferguson, W. (1986). Radio tracking of problem fruit bats (*Rousettus aegyptiacus*) in the Transvaal with notes on flight and energetics. *Zeitschrift Fur Saugetierkunde*, 51, 205–208.
- Kunz, T. H., de Torre, E. B., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. *New York Academy of Science*, 1223, 1–38. <https://doi.org/10.1111/j.1749-6632.2011.06004>
- Lewis, F., Butler, A., & Gilbert, L. (2011). A unified approach to model selection using the likelihood ratio test. *Methods in Ecology and Evolution*, 2, 155–162. <https://doi.org/10.1111/j.2041-210X.2010.00063>
- Lucan, R. K., Bartonicka, T., Jedlicka, P., Rerucha, S., Salek, M., Cizek, M., Nicolaou, H., & Horacek, I. (2016). Spatial activity and feeding ecology of the endangered northern population of the Egyptian fruit bat (*Rousettus aegyptiacus*). *Journal of Mammalogy*, 97, 815–822. <https://doi.org/10.1093/jmammal/gyw014>
- Maroyi, A. (2018). *Syzygium cordatum hochst.* Ex Krauss: An overview of its ethnobotany, phytochemistry and pharmacological properties. *Journal of Synthetic Chemistry and Natural Product Chemistry*, 23(5), 1084. <https://doi.org/10.3390/molecules23051084>
- Mickleburgh, S. P., Hutson, A. M., & Racey, P. A. (2002). A review of the global conservation status of bats. *Oryx*, 36, 18–34.
- Monadjem, A., Taylor, P. J., Cotterill, F. P. D., & Schoeman, M. C. (2020). *Bats of southern and Central Africa: A biogeographic and taxonomic synthesis* (2nd ed.). Wits University Press. <https://doi.org/10.18772/22020085829>
- Mucina, L., & Rutherford, M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19 south African national biodiversity institute.
- Naranjo, M. E., Rengifo, C., Pascual, J., & Soriano, P. J. (2003). Effect of ingestion by bats and birds on seed germination of *Stenocereus griseus* and *Subpilocereus repandus Cactaceae*. *Journal of Tropical Ecology*, 19, 19–25. <http://www.jstore.org/stable/4091821>

- Northam, F. E., & Calliham, R. H. (1994). Interpreting germination results based on differing embryonic emergence criteria. *Weed Science*, 42(3), 474–481. <https://doi.org/10.1017/S0043174500076797>
- Nyhus, P. J. (2016). Human-wildlife conflict and coexistence. *Annual Review of Environment and Resources*, 41, 143–171.
- Picot, M., Jenkins, R. K. B., Ramilijaona, O., Racey, P. A., Stephanie, M., & Carrie'Re, S. M. (2007). The feeding ecology of *Eidolon dupreanum* (Pteropodidae) in eastern Madagascar. *African Journal of Ecology*, 45, 645–650. <https://doi.org/10.1111/j.1365-2028.2007.00788>
- Pothasin, P., Compton, S. G., & Wangpakapattanawong, P. (2014). Riparian *Ficus* tree communities: The distribution and abundance of riparian fig trees in northern Thailand. *PLoS One*, 9(10), e108945. <https://doi.org/10.1371/journal.pone.0108945>
- Price, V. (2013). *Trouble in paradise: Mapping human-wildlife conflict in the western Indian Ocean*. Unpublished MSc thesis, Imperial College, London, UK.
- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Raharimihaja, T. E. A., Rakotoarison, J. L. M., Racey, P. A., & Andrianaivoarivelo, R. A. (2016). A comparison of the effectiveness of methods of deterring Pteropodid bats from feeding on commercial fruit in Madagascar. *Journal of Threatened Taxa*, 8(13), 9512–9524. <https://doi.org/10.11609/jott.2688.8.13.9512-9524>
- Raji, I. A., & Downs, C. T. (2021). *Ficus*-frugivore interactions, especially in areas of land-use change, in Africa: A systematic review. *Acta Oecologica*, 113, 103774. <https://doi.org/10.1016/j.actao.2021.103774>
- Relox, R., Florece, L. M., Baril, J. A., & Coladilla, J. (2014). Assessment of fruit bats and their food preferences in Mt. Apo National Park, Kidapawan City, North Cotabato, Philippines. *Journal of Environmental Sciences and Management*, 17(1), 12–20. https://doi.org/10.47125/jesam/2014_1/02
- Richter, H., & Cumming, G. (2008). Food availability and annual migration of the straw-coloured fruit bat (*Eidolon helvum*). *Journal of Zoology*, 268, 35–44. <https://doi.org/10.1111/j.1469-7998.2008.00425>
- Robertson, A. W., Trass, A., Ladley, J. J., & Kelly, D. (2006). Assessing the benefits of frugivory for seed germination: The importance of the deinhibition effect. *Functional Ecology*, 20, 58–66. <https://doi.org/10.1111/j.1365-2435.2005.01057>
- Rollinson, D. P., Coleman, J. C., & Downs, C. T. (2013). Seasonal differences in foraging dynamics, habitat use and home range size of Wahlberg's epauletted fruit bat in an urban environment. *Africa Zoology*, 48(2), 340–350. <https://doi.org/10.3377/004.048.0218>
- Rossaneis, B. K., Reis, N. R., Bianchini, E., & Pimeta, J. A. (2015). Seed germination after passing through gastrointestinal tract of bats (Chiroptera, Phyllostomidae). *Semina*, 36(2), 3–14.
- Scanlon, A. T., Petit, S., Tuiwawa, M., & Naikatini, A. (2014). High similarity between a bat-served plant assemblage and that used by humans. *Biological Conservation*, 174, 111–119. <https://doi.org/10.1016/j.biocon.2014.03.023>
- Seltzer, C. E., Ndangalasi, H. J., & Cordeiro, N. J. (2013). Seed dispersal in the dark: Shedding light on the role of fruit bats in Africa. *Biotropica*, 45(4), 450–456. <https://doi.org/10.1111/btp.12029>
- Serio-Silva, J. C., & Rico-Gray, V. (2002). Interacting effects of forest fragmentation and howler monkey foraging on germination and dispersal of fig seeds. *Oryx*, 36, 266–271.
- Sileshi, G. W. (2012). A critique of current trends in the statistical analysis of seed germination and viability data. *Seed Science Research*, 22, 145–159. <https://doi.org/10.1017/S0960258512000025>
- Snoder, E. R. (2010). Effects of epauletted fruit bats (*Epomophorus crypturus* an *Epomophorus wahlbergi*) on the seed germination of sycamore fig trees (*Ficus sycomorus*) in the Kruger National Park, South Africa. M.Sc. Thesis, University of Northern Colorado, Greeley, USA, 110.
- Steinbrechter, T., & Leubner-Metzger, G. (2018). Tissue and cellular mechanics of seeds. *Current Opinion in Genetics & Development*, 51, 1–10. <https://doi.org/10.1016/j.gde.2018.03.001>
- Symonds, M. R. E., & Moussalli, A. (2010). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65, 13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Tidemann, C. R., & Nelson, J. E. (2004). Long-distance movements of the grey-headed flying fox (*Pteropus poliocephalus*). *Journal of Zoology*, 263(2), 141–146.
- Tollington, S., Kareemun, Z., Augustin, A., Lallchand, K., Tatayah, V., & Zimmermann, A. (2019). Quantifying the damage caused by fruit bats to backyards lychee trees in Mauritius and evaluating the benefits of protective netting. *PLoS One*, 14(8), e0220955. <https://doi.org/10.5061/dryad.5q041fq>
- Tshililo, F. P., Savage, M. J., & Moeletsi, M. E. (2021). Rainy season characteristics for the Luvuvhu River catchment, South Africa. *Water SA*, 47, 480–487. <https://doi.org/10.17159/was/2021.v47.i4.3677>
- van der Pijl, L. (1957). The dispersal of plants by bats (chiropterchory). *Acta Botanica Neerlandica*, 6, 291–315. <https://doi.org/10.1111/j.1438-8677.1957.tb00577>
- van Mele, P., Camara, K., & Vaysierres, J. F. (2009). Thieves, bats and fruit flies: Local ecological knowledge on the weaver ant *Oecophylla longinoda* in relation to three 'invisible' intruders in orchards in Guinea. *International Journal of Pest Management*, 55, 57–61. <https://doi.org/10.1080/09670870802450276>
- van Toor, M. L., O'mara, M. T., Abedi-Lartey, M., Wikelski, M., Fahr, J., & Dechmann, D. K. N. (2019). Linking colony size with quantitative estimates of ecosystem services of African fruit bats. *Current Biology*, 29, 225–240. <https://doi.org/10.1016/j.cub.2019.02.033>
- van Wyk, A. E., & Smith, G. F. (2001). *Regions of floristic endemism in southern Africa: A review with emphasis on succulents*. Umdaus Press.
- Voigt, C. C., Kelmy, D. H., Bradley, B. J., & Ortmann, S. (2009). Dietary analysis of plant-visiting bats. In T. H. Kunz & S. Parsons (Eds.), *Ecological and behavioral methods for the study of bats* (pp. 593–609). Johns Hopkins University Press.
- Willems, E. P., Barton, R. A., & Hill, R. A. (2009). Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behavioral Ecology*, 20, 985–992.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Mphethe, V., Weier, S., Westphal, C., Linden, B., Swanepoel, L., Parker, D., & Taylor, P. (2023). Epauletted fruit bats prefer native plants and contribute to seed dispersal in a South African agricultural landscape. *African Journal of Ecology*, 61, 399–410. <https://doi.org/10.1111/aje.13132>