Fruit bat diet, foraging ecology and seed dispersal in the Vhembe Biosphere Reserve.

Thesis submitted to the Department of Biological Sciences,

Faculty of Science, Engineering and Agriculture, University of Venda, in the fulfilment of the requirements for the Degree of

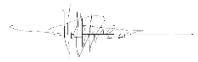
Doctor of Philosophy in

Zoology

by

Vusani Mphethe

(Student No: 11582175)



Faculty of Science, Engineering and Agriculture

University of Venda

Thohoyandou, Limpopo

South Africa

Promoter: Prof. L. H. Swanepoel

Co-promoter: Prof. P. J. Taylor

2nd Co-promoter: Prof. C. Westphal

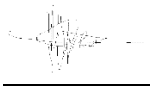
3rd Co-promoter: Prof. D. Parker

4th Co-promoter: Dr S. Weier

February 2023

Declaration

I, VUSANI MPHETHE, hereby declare that the thesis for the degree of Doctor of Philosophy in Zoology submitted by me at the Faculty of Science, Engineering and Agriculture at University of Venda, has not been previously submitted for a degree at this University or any other University, that it is my own work in design and execution and that all referenced material contained therein has been duly acknowledged.

Signature : 

Date : 25/02/2023

Publication timeline and disclaimer

Please note that chapter two to four of this thesis were written as stand-alone papers (see below), and therefore some repetition was unavoidable. The following chapter (s) are accepted for publication in journals:

Chapter 2: Mphethe, V., Weier, S., Westphal, C., Linden, B., 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, 00, -12. https://doi.org/10/1111/aje.13132

Acknowledgements

Many thanks to litchi growers in the Levubu study area for their support and providing access to their orchards, particularly Dennis Gilbert, Fritz Ahrens, Herman de Jagger, Shandukani Mulaudzi, and Mandy Hugo. I thank the Subtropical Fruit Association of South Africa (SUBTROP), more especially Andries Bester for introducing me to litchi farmers in Tzaneen, and the small-scale litchi farmers in the Vhembe region who have shown interests on bats and participated in this study. I would also like to thank Prof. Jan Crafford (Kutetsha Research Camp) for the hospitality and granting us permission to sample in his property, to Dave Dewsnap (Goro Game Reserve), for allowing us access in their property. Dr. Birthe Linden from Lajuma Research Centre is also thanked for providing seed reference library and help in seed identification. I would also thank the Agroecology Department of Functional Agrobiodiversity of the University of Gottingen (Germany) as well as Prof. Catrin Westphal for their support. Many thanks to Murunwa Nelufule, Claire Arne, and my cousin Nkhumeleni Nkhwamatumba for helping me with data collection, and to Mr. Tshiambara and his school principal from Mavhungu Andries Secondary School for helping me to locate Mangwele cave in Tshakhuma, and the Tshakhuma Tribal Office for granting us access to the cave. Many thanks to Prof. Lourens Swanepoel from the University of Venda for designing and construction of exclusion cages. I am more than greatful to my promoters Prof. Lourens Swanepoel, Prof. Peter Taylor, Prof. Dan Parker, Prof. Catrin Westphal, and Dr. Sina Weier for their inputs, support and encouragement throughout my studies. Last but not least, I would like to thank my partner and mother for their support.

Funding: This work was supported by the University of Venda and National Research Foundation (NRF) and the Department of Science and Technology (DST), through the SARCHI Research Chair on Biodiversity Value & Change in the Vhembe Biosphere Reserve; The German Academic Exchange Service – DAAD [grant number: 57531828].

Table of contents

List of Tables

List of Figures

List of Appendices

Overall abstract

Agricultural intensification, and a rapid human population growth have resulted in increased human wildlife contact. In the case of fruit bats, conflict with commercial fruit farmers has been a leading contributor to a decline of bat species populations, despite the vital ecosystem service of seed dispersal provided by fruit bats. Conflict between fruit bats and fruit farmers often stems from perceived or actual damage to their crops, especially during the harvest season. Such conflict often leads to the persecution of fruit bats, either legally or illegally. Therefore, a proactive assessment of bats diet in agroecosystems is important. South Africa is one of the major producers of litchi and its litchi industry is well established and continues to grow. This study provides insight into the diet, foraging behavior, and ecosystem service of seed dispersal of fruit bat species in litchi orchards and natural habitats to advise on management strategies on how to reduce crop damage. It also assesses crop raiding by fruit bats and other crop raider animals, and their activity patterns in response to litchi abundance during the harvest season using camera traps. This study also used a vertebrate exclusion experiment to quantify the effect of excluding crop raiders on yield, as well as a questionnaire survey to quantify the perceived damage in litchi orchards. The study was conducted in the subtropical fruit growing area of Levubu and the natural habitats of the Soutpansberg, Limpopo province, South Africa.

An introduction to the order Chiroptera and important fruit bats ecosystem service of seed dispersal as well as the disservice of crop depredation in agroecosystems is provided in **Chapter One**.

Chapter Two, bats were captured with mist nest in both agricultural and natural habitats during the litchi pre-harvest and harvest seasons. We sampled the litchi orchards as well as natural habitats from February 2018 to November 2020 and used GIS and R (ggplot2, iNEXT, lme4) to analyse fruit bats diet, their effect on seeds germination and habitat use with respect to litchi fruit abundance. Results show that fruit bat diet was dominated by wild fruit species (95%) during the litchi harvest season (December) when fruit bats are perceived to be feeding on litchi fruits. Ficus (*Ficus* spp.) seeds collected as fruit bats spit-out seeds had significantly lower germination rates than regular seeds, but a significantly lower germination latency, and a similar pattern was also observed for quinine tree (*Rauvolfia caffra*). Our results suggested that fruit bats inhabiting litchi orchards and surrounding natural vegetation feed primarily on wild fruits due to the high percentage of natural vegetation in our study area, which support the importance of natural orchard edges in mitigating crop raiding.

Chapter Three, we mounted 10 camera traps (from October 2019 to December 2020) on two litchi orchards for assessing fruit bats and other crop raider animal species richness and activity patterns in response to litchi abundance during litchi harvest season. Six time-triggered canopy camera traps were mounted (6m above the ground) to monitor the animals visiting litchi tree canopies during litchi pre-harvest (October/November) and harvest sessions (December). Additionally, four motion-triggered camera traps were mounted 30 cm above the ground to monitor animals visiting the litchi trees at the ground level. We used Digikam software to tag images and R (ggplot2, iNEXT, lme4, overlap, RSQLite) to analyse species richness, Relative abundance Index (RAI), and crop raider activity patterns. We recorded a significantly higher species richness index during the harvest season (December) compared to litchi pre-harvest season (October/November). Crop raider species richness was lower compared to incidentally observed species during the litchi harvest season. Fruit bats (which could not be assigned to either *Epomophorus* or *Rousettus* genus) recorded lower activity (RAI (of 2.49) compared to Dark-capped Bulbul (*Pycnonotus tricolor*; RAI (43.44)). Lastly, fruit bats did not show/exhibit any change in seasonal activity between the litchi pre-ripe and ripe seasons.

As reported in **Chapter Four**, we collected the litchi yield data on both vertebrate exclusion trees (caged) and paired open control trees during the December/January harvest season between 2019 and 2020, to quantify the effect of excluding crop raider vertebrates, weather, and insect damage on yield. We constructed a total of six vertebrate exclusion cages on two litchi orchards, each enclosing one litchi tree and paired them with open control trees marked with a tapper. Additionally, a questionnaire survey was conducted in **Chapter Four** from both commercial and small-scale litchi farmers to quantify the perceived damage caused by crop raiders and later compared the results to the total yield for trees inside the exclusion cages and paired open control trees. Our litchi yield results show that open control trees produced significantly higher yield than caged trees, which is contrary to our hypothesis. There was also a weak but non-significant trend towards higher vertebrate damage on control trees compared to caged trees. Questionnaire survey results revealed that weather (sun/rain) and monkeys were the main cause of damage in litchi orchards, when compared to fruit bats, and there was a strong agreement among farmers that the damage varied by vertebrate groups. Farm type (commercial versus small-scale) also show statistically significant difference in the perceived damage caused by bats, birds, insects, monkeys, weather and wild pigs. The results of our study also show lower crop raiding incidence were reported for fruit bats.

In summary, **Chapter Five** concludes that fruit bats prefer to feed on wild fruits over commercially cultivated fruits such as litchi, and potentially provide ecosystem service of seed dispersal, and that remnant natural vegetation at the orchard edges are important food sources, and assist in mitigating crop raiding, and need to be maintained or restored. The study also shows that fruit bats are not crop raiders of litchi fruits, and do not change their seasonal foraging activity in respond to litchi abundance during the litchi harvest season, as believed by farmers. However, further research on fruit bats crop raiding must be conducted in an area with known abundance of colonial species like *Rousettus aegyptiacus,* a known global pest of litchi crop. Additionally, the use of radio tracking should be considered, and could provide insight into fruit bats habitat use. Our study further revealed that vertebrate exclusions did not increase litchi yield, and that weather and monkeys were the main cause of damage when compared fruit bats. As a result, this study provides information to farmers on fruit bat`s important ecosystem service of seed dispersal and the benefit of maintaining natural orchard edges.

Chapter 1: The need for fruit bat conservation for their ecosystem services provision in different land use zones

An introduction to the order Chiroptera

Bats (order Chiroptera) are the only flying mammals, and there are over 1400 species of 19 families globally (Monadjem *et al*., 2020). Chiroptera (bats) is the most diverse mammal group after Rodentia (rodents) and account for one-fifth of mammalian diversity on the planet (Teeling *et al*., 2012). Bats are long-lived mammals with most females producing one pup or twins per year (Barclay and Harder, 2003). Bats are found on all continents except Antarctica, and most islands due to extreme weather conditions (Monadjem *et al*., 2020). In southern Africa, there are over 120 species of bats belonging to eight families. The family Pteropodidae are fruit eating bats with over 30 species of which 21 in 11 genera have been recorded in southern Africa (Hassanin *et al*., 2015). Fruit bats rely on eyesight and sensory organs to navigate around their environment, and only one species in the genus *Rousettus* has developed a distinct form of echolocation (Neuweiler, 1990).

Ecosystem services provided by fruit bats

Fruit bats provide vital ecosystem services including seed dispersal and pollination (Fujita and Tuttle, 1991; Kunz *et al*., 2011). Fruit bats are known to pollinate about 528 species of flowering plants globally, with 20% of plant species in Tanzania (Africa) relying on seven species of fruit bats for seed dispersal (Fleming *et al*., 2009; Seltzer *et al*., 2013). In west Africa, important medicinal and commercial plants such as baobabs (*Adansonia digitata*), and sausage trees (*Kigelia africana*) are known to be pollinated by fruit bats (Jaeger, 1945; Harris and Baker, 1959). Pteropodids are also responsible for propagating economically important plant species which produce vital resources and products including fruits, drinks, food, ornamental plants, timber, dye, fibres, tannins, medicines, and animal fodder (Fujita and Turtle, 1991). In Zimbabwe, pteropodids were observed pollinating flowers of baobab trees (Dr Sarah Venter personal communication). However, in South Africa, only hawk moths (*Sphingidae*) have been observed as frequent visitors/pollinators of baobab flowers (Taylor *et al*., 2020). In South Africa, epauletted fruit bats have shown much preference on *Ficus* spp. fruits, thereby enhancing seed germinability through ingestion (Snode, 2010; Bonaccorso *et al*., 2014). The presence of fruit bats in different land uses is therefore important for seed dispersal of indigenous natural plants and hence improve seed germinability.

Fruit bats ecosystem disservices

Contrary to ecosystem services, fruit bats also provide disservices in the form of fruit depredation, a global problem especially in agroecosystems (Aziz *et al*., 2016). Pteropodids have been reported to raid fruit orchards of commercially cultivated fruits such as litchi (*Litchi chinensis*), mango (*Mangifera indica*), and papaya (*Carica papaya*) and cause significant damage (Van Mele *et al*., 2009; Weber *et al*., 2015; Tollington *et al*., 2019). Litchi and mango damage from fruit bats (*Pteropus rodricensis* and *Pteropus niger*) was estimated at 36% and 42% in Mauritius (Price, 2013, Tollington *et al*., 2019). In Australia, farmers reported having lost 90% of their crops from flying fox depredation (Dewhurst, 1998; Aziz *et al*., 2016), while in South Africa, *R. aegyptiacus* were reported to cause a significant damage in litchi orchards (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986).

Threats to fruit bats

Fruit bats provide valuable ecosystem services of pollination and seed dispersal around the world (Fujita and Tuttle, 1991; Fleming *et al*., 2009; Kunz *et al*., 2011). Despite all these important services, fruit bats are blamed for outbreaks of frightening viral diseases such as Ebola, Rabies, Hendra and Nipah, which results in the destruction of many bat populations due to fear, although there is sufficient scientific evidence that not a single guano mine cave had been reported to have an outbreak (Adams and Pedersen, 2013). Fruit bat overhunting in Africa, Asia and the Pacific and Indian Ocean Islands for consumption or profit, has resulted in a major decline in populations (Mickleburgh *et al*. 2011). Bats are blamed for massive crop loss in both commercial and subsistence farming resulting to legal culling in many parts of the world due to lack of ecological knowledge and benefits these animals provide to the environment (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986; Adams and Pedersen, 2013; Tollington *et al*., 2019). Environmental degradation is one of the major threats to fruit bats due to habitat destruction for agricultural expansion or residential/industrial development resulting to their natural habitat being destroyed, and human-wildlife conflict (Ladan, 2014). About 15% of southern African bat species are listed as data deficient by the IUCN, which is concerning since there is lack of knowledge about bats (Monadjem *et al*., 2020).

The South African litchi industry

In South Africa, 1 731 ha of land is covered by commercial litchi orchards, with 514 ha in the Limpopo Province, 1 108 ha in Mpumalanga and 109 in KwaZulu-Natal (Begermann, 2014). South Africa produces 10 444 tons of litchis annually during good season which is sold locally as fresh fruit at the Johannesburg market, and about 5 613 tons of those exported annually (DAFF, 2018). Grove *et al*., (2014) reported that in South African litchi (*Litchi chinensis*) plantations most of the damage is caused by arthropod pests such as the litchi moth (*Cryptophlebia peltastica*), false codling moth (*Thaumatotibia leucotreta*), and fruit flies (*Ceratitis* spp.).

Rationale of this study

Human-wildlife conflict between litchi farmers and Pteropodids in the subtropical area of South Africa has resulted in fruit bats persecution due to the damage on litchi crops (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986). Therefore, this study aims to provide knowledge on the positive and negative roles (services and disservices) of fruit bats in a multifunctional landscape in Levubu containing fruit crops and natural areas.

Study area

This study was conducted within the Vhembe Biosphere Reserve, which was declared by UNSECO as a recognized centre of endemism and species diversity (Mostert *et al*., 2008).

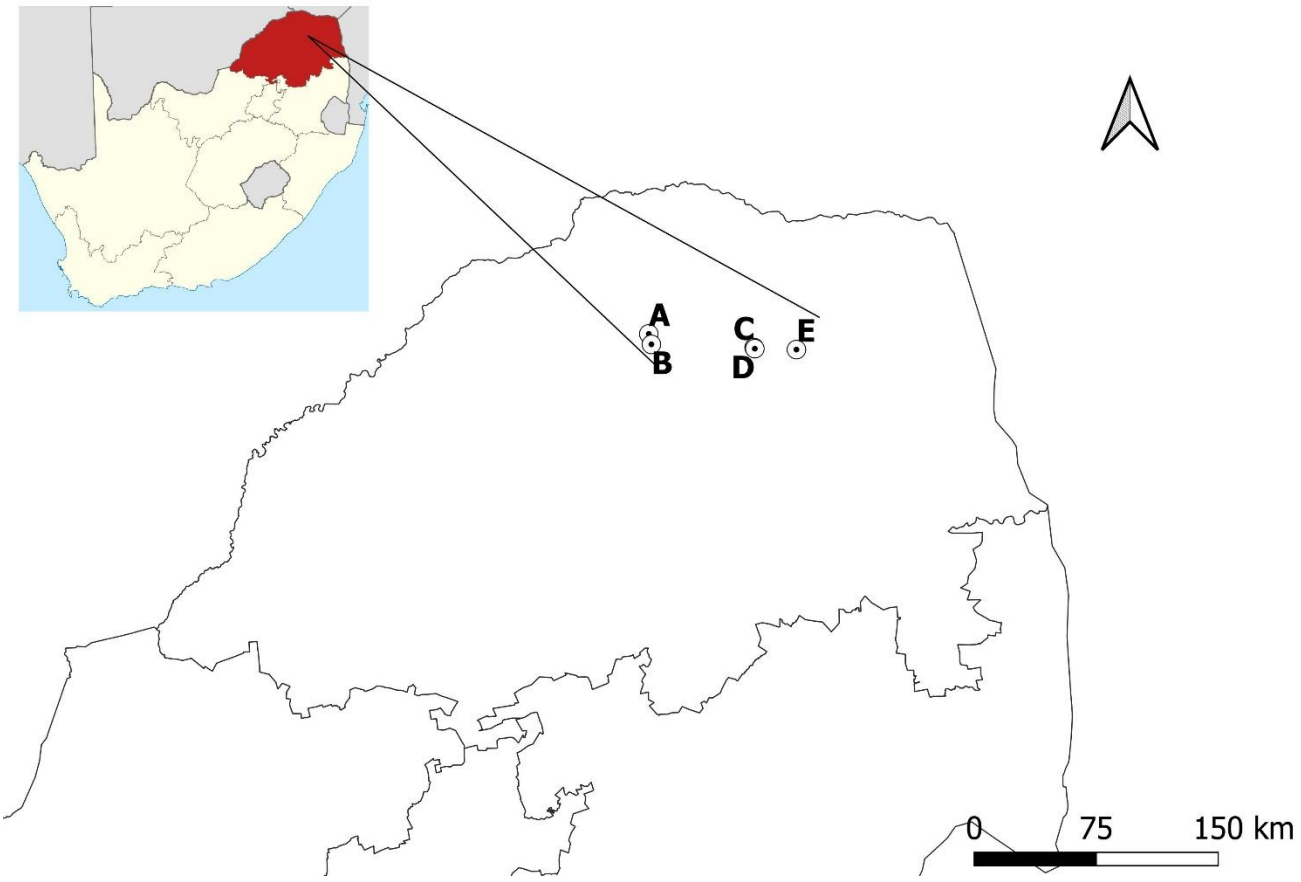


Figure 1 Map showing the study area in the Vhembe Biosphere Reserve including the Levubu subtropical crop growing area and the Soutpansberg natural habitats (A = Goro Game Reserve, B = Lajuma Research Centre and the Kutetsha Research Camp, C = Neuhoff Farm, D = Rionde Fruit Farm, E = Tshakhuma Laatsgevonden Farms).

This study was conducted in the Vhembe Biosphere Reserve which includes the Soutpansberg mountain range, a known hotspot for plant and animal endemism (Hahn, 2017; Cooper-Bohannon *et al*., 2016). The area sampled includes Bergplaats, Goro and Lajuma Research Centres which form part of the study area and situated right at the top of this mountain range and characterized by different vegetation types from the Afro-montane forests, sparse Kalahari sand-type xeric scrub communities and a unique Soutpansberg mountain bushveld (Mucina and Rutherford, 2006). Laatsgevonden is situated in the Levubu subtropical fruit growing area, located at the foothill of the Soutpansberg mountain range, and the Luvuvhu river flowing though the Levubu valley. The area is dominated by extensive monoculture of macadamias, pecan nuts, bananas, pine, and blue gum

plantation, and encompasses our second study site, surrounded by litchi, macadamia, mangoes, guava, banana, and natural vegetation with a higher diversity of wild fruits such as *Ficus* (Figure 1). Fruit bats have been documented to feed on commercial fruits such as guava, litchi, mangoes, and papayas (Jacobsen and du Plessis, 1976; Fleming *et al*., 2009, Monadjem *et al*., 2020). Fruit bats depredation on commercial fruits has led to fruit bat/farmer conflict in many parts of the world including Australia, Israel, Mauritius, and South Africa, resulting in a massive decline in population (Tollington *et al*., 2019). However, fruit bats provide vital ecosystem services of pollination, forest regeneration, and seed dispersal of both indigenous and exotic plant species (Fujita and Turtle, 1991; Kunz *et al*., 2011).

The thesis aims and objectives

This thesis aims to get an insight into fruit bat habitat use, seasonal effects, ecosystem services and disservices in a multifunctional landscape in Levubu (agricultural) and Soutpansberg (natural area), in order to provide the knowledge to litchi farmers on fruit bat diet and habitat use with respect to crop damage and advise on management strategies on how to reduce such problem using an integrated pest management approach (IPM).

The objectives for chapters two, three and four were as follows:

Chapter Two reports on fruit bat diet, habitat use, seed dispersal and foraging behaviour in relation to ripe litchi fruits in order to advise farmers on the possible management plan to reduce crop raiding during litchi fruiting season. We hypothesized that litchi would predominate the diet of fruit bats over natural food plants during the litchi fruiting season, when bat diet was sampled in the vicinity of litchi orchards compared with samples from natural areas. We further predicted that seeds from fruit bat spit outs might germinate faster than untreated seeds. Lastly, we predicted that GPS tagged fruit bats would spend most of their time foraging over ripe litchi orchards litchi fruiting season.

Chapter Three aims to provide an insight on crop raiders` species richness and activity patterns in response to litchi fruit abundance, using camera traps mounted at ground level and canopy level. We predicted that litchi harvest season would have the highest activity of crop raiders in response to food abundance compared to the litchi pre-fruiting season. We also hypothesized that litchi crop abundance would have a positive influence on species richness of both crop raiders and non-crop

raiders/incidentally observed species (i.e., rotting litchi fruits attract flies and hence insectivorous birds) within farms as well as between the two farms. We further predicted that crop raider species richness would be higher than non-crop raider species recorded at the ground and canopy level in response to the abundance of ripe litchi fruits. Lastly, we predicted that crop raider species would spend more time foraging over ripe litchi orchards during December when the fruits are ripe, compared to the preceding months of October and November when the fruits are not ripe.

Chapter Four aims to quantify the damage caused by fruit bats, birds, and primates, using vertebrate exclusion experiments on two litchi farms over a period of two years. We further aimed to compare the actual litchi crop damage to perceived damage by conducting questionnaire surveys. We hypothesized that the absence of crop raiding vertebrates such as bats, birds, and monkeys would decrease damage to litchi fruits. we therefore also predicted that caged litchi trees would produce higher yields than control (un-caged) trees. We further predicted that farmers might perceive damage by fruit bats to be higher than other vertebrates. Finally, we hypothesized that the absence of crop raiding vertebrates such as fruit bats and monkeys would decrease damage to litchi fruits, but by removing insectivorous birds and bats would increase the damage. We therefore predicted that, while removal of large crop raiders may increase yield for caged litchi trees, removal of insectivorous bats and birds may decrease yield due to insect damage.

References

ADAMS, R. A. & PEDERSEN, S. C. (2013) Bat Evolution, Ecology, and Conservation. *New York, Springler*

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*, 377-426. doi:10.1007/978-3-319-25220-9_13

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. doi:10.3161/150811014X683255

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. doi:10.4404/hystrix-27.1-11722

DAFF. (2018). Litchi production guidelines. Republic of South Africa, available online at https://www.dalrrd.gov.za.

DEWHURST. (1998). Correspondence from Queensland Fruit and Vegetable Growers to DPI. Quoted by Teagle S 2002 op cit

FLEMING, T. H., GEISELMAN, C. & KRESS, W. J. (2009). The evolution of bat pollination – a phylogenetic perspective. *Annals of Botany*, 104, 1017-1043. doi:10.1093/aob/mcp197, available online at www.aob.oxfordjournals.org

FUJITA, M. S. & TUTTLE, M. D. (1991). Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology*, 5, 455–463.

GROVE, T., SCHOEMAN, S. & BEER, M. S. (2014) Arthropod pests of litchi in South Africa, *Acta Horticulturae*, 1029, 409-416

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

HARRIS, B. J. & BAKER, H. G. (1959). Pollination of flowers by bats in Ghana. *Niger. Field* 1, 24, 154–159.

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 TORREZ, E. B., BAUER, D., LOBOVA, T. & FLEMING, T. H. (2011). Ecosystem services provided by bats. *New York Academy of Science*, 1223, 1-38. doi:10.1111/j.1749-6632.2011.06004.

LADAN, S. I. (2014) Examining human wildlife conflict in Africa. In: International conference on biological, civil and environmental engineering.

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*, Johannesburg, South Africa. https//dx.doi.org10.18772/22020085829

MOSTERT, T. H. C., BREDENKAMP, G. J., KLOPPER, H. L., VERWEY, C., MOSTERT, R. E. & HAHN, N. (2008). Major vegetation types of the soutpansberg conservancy and the blouberg nature reserve. *South Africa. Koedoe*, 50, https://doi.org/10.4102/koedoe.v50i1.125

MUCINA, L. & RUTHERFORD, M. C. (2006). The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19 South African National Biodiversity Institute, Pretoria, South Africa.

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. *Biotropical*, 45 (4). doi: 10.1111/btp.12029

SNODE, 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

TAYLOR, P. J., MATAMBA, E., STEYN, J. N., NANGAMMBI, T., ZEPEDA-MENDOZA, M. L. & BOHMANN, K. (2017). Diet determined by next generation sequencing reveals pest consumption and opportunistic foraging by bats in macadamia orchards in South Africa. *Acta Chiropterologica*, 19, 239–254. https://doi.org/10.3161/15081109ACC2017.19.2.003

TAYLOR, P. J., VISE, C., KRISHNAMOORTHY, M. A., KINGSTON, T. & VENTER, S. (2020). Citizen Science Confirms the Rarity of Fruit Bat Pollination of Baobab (*Adansonia digitata*) Flowers in Southern Africa. *Diversity*, 12 (106). doi:10.3390/d12030106

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. doi:10.5061/dryad.5q041fq

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. *Int J Pest Manage*, 55, 57–61

WEBER, N., DUENGKAE, P., FAHR, J., et al. (2015). High-resolution GPS tracking of Lyle's flying fox between temples and orchards in central Thailand. *J Wildl Manage*, 79, 957–968

Chapter 2: Epauletted fruit bats prefer native plants and contribute to seed dispersal in a South African agricultural landscape

Vusani Mphethe[1,2], Sina Weier[2,3], Catrin Westphal[4], Birthe Linden[2,5], Lourens Swanepoel[1,2], Daniel Parker[6] and Peter Taylor[2,3].

[1]Department of Biological Sciences, Faculty of Science, Engineering and Agriculture, Thohoyandou, 0950, South Africa

[2]SARChI Chair on Biodiversity Value and Change, Faculty of Science, Engineering and Agriculture, Private Bag X5050, Thohoyandou, 0950, South Africa

[3]Department of Zoology & Entomology & Afromontane Research Unit, University of the Free State, QwaQwa Campus, Private Bag X13, Phuthaditjhaba, 9866, South Africa

[4]Functional Agrobiodiversity, Georg-August-University Göttingen, Grisebachstr. 6, 37077 Göttingen, Germany

[5]Lajuma Research Centre, Louis Trichardt, Limpopo Province, South Africa

[6]School of Biology and Environmental Sciences, University of Mpumalanga, Mbombela, 1200, South Africa

Published: African Journal of Ecology

Abstract

Fruit bats provide vital ecosystem services through seed dispersal aiding secondary forest regeneration. However, fruit bat species are often subjected to persecution by fruit growing farmers due to perceived and actual crop damage. In this study, we investigated the dietary components of Wahlberg`s epauletted fruit bat (*Epomophorous wahlbergi*), Peters`s epauletted fruit bat (*E. crypturus*), and Egyptian fruit bat (*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 (SO) 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.

Key words: Bat diet, agriculture, litchis, habitat use, seed dispersal, seed germination

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 consist of a wide range of wild indigenous tree species (Seltzer *et al*., 2013; Bonaccorso *et al*., 2014; Monadjem *et al*., 2020). In the Philippines, the Musky Fruit Bat (*Ptenochirus jagori*), Philippine Pygmy Fruit Bat (*Haplonycteris fischeri*), and Lesser Musky Fruit Bat (*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 (Rollinson *et al*., 2013; Bonaccorso *et al*., 2014). Fruit bats may feed on commercial fruits, including mango (*Mangifera indica*), pawpaw (*Asimina triloba*), guava (*Psidium guajava*), litchi (*Litchi chinensis*), banana (*Musa acuminata*), date (*Phoenix dactylifera*) and other exotic species such as syringa berry (*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 (*P. rodricensis*) raiding backyard litchis and mango trees caused around 36% to 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 the associated losses, can lead to human-wildlife conflict and subsequent persecution of fruit bats (Fujita and Tuttle, 1991; Kunz *et al*., 2011; Aziz *et al*., 2016). As such, it remains important to investigate factors leading to fruit raiding behaviour and the extent of damage. This research priority is especially important for Egyptian fruit bats which are perceived as potential crop raiders in commercial litchi farms of 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) and the former were more prevalent in natural foods. This scenario suggests that fruit bats might not always pose a significant

risk to commercial fruit production where fruit is picked/harvested unripe, as they generally prefer ripe fruit (Fleming *et al*., 2009; Monadjem *et al*., 2020).

In this study, we used three fruit bat species Wahlberg`s epauletted fruit bat (*Epomophorous wahlbergi*), Peters`s epauletted fruit bat (*E. crypturus*) and Egyptian fruit bat (*R. aegyptiacus*) to investigate fruit raiding behaviour in an agricultural matrix dominated by fruit orchards. Fruit bats are an ideal study organism in this context 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 (Fujita and Tuttle, 1991; Kunz *et al*., 2011; Bonaccorso *et al*., 2014; Fahr *et al*., 2015; Abedi-Lartey *et al*., 2016). 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, fibers, tannins, medicines, and animal fodder (Fujita and Tuttle, 1991). Fruit bats (*Pteropodidae*) and flying foxes (*Pteropus*) in Africa and Australia can cover up to 1500 km during migration, while foraging and dropping different varieties of seeds in flight (Tidemann and Nelson, 2004; Richter and Cumming, 2008). Similarly, telemetry work has shown Wahlberg`s epauletted fruit bat travelling over 13 km 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 bat flew 24 km 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 fertilization 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 sycomorus*) seeds passing through the gastrointestinal tract of Wahlberg`s epauletted fruit bats have 88-100% germination success in sterile petri dishes.

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) generas (Aziz *et al*., 2021). Fig trees are important keystone species and food resource which sustain populations of fruigivores that feed on their fruits including fruit bats (Pothasin *et al*., 2014; Bonaccorso *et al*., 2014). Similarly, *Syzygium* is also consumed by fruit bats (Monadjem *et al*., 2020), hence an important plant to treat diseases such as malaria, tuberculosis, sexually transmitted

infections (STIs) burns and gastro-intestinal disorders (Maroyi, 2018). In Colombia, fruit bats were reported to facilitate ecosystem services of seed dispersion as well as increased soil fertility in agroecosystems (Enriquez-Acevedo *et al*., 2020). In addition, fruit bats were documented to disperse approximately 20% of both widespread and endemic trees in East Usambara Mountains of Tanzania (Seltzer *et al*., 2013). In Ghana, GPS-tracked straw-coloured fruit bat (*Eidolon helvum*) retained ingested seeds for extended periods 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 hypothesized that litchis would predominate in the diet of fruit bats (Wahlberg`s epauletted fruit bat, Peters`s epauletted fruit bat and Egyptian fruit bat 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 and 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 1142 m above sea level, and is about 586 ha in size (Figure 2) and is characterized by Northern Mistbelt Forest, Soutpansberg Mountain Bushveld and Soutpansberg Summit Sourveld (Mucina and Rutherford, 2006). The Luvhondo Nature Reserve consists of several privately owned properties and is approximately 4300 ha in size. Luvhondo Nature Reserve is situated on the Soutpansberg Mountain Range, a recognised centre of plant endemism (Van Wyk and Smith, 2001; Hahn, 2017) and a centre of floristic diversity (Hahn, 2019). The Soutpansberg is further regarded a hotspot for bat species (Cooper-Bohannon *et al*., 2016). The study site receives a mean annual rainfall of 724 mm with a summer rainy season between December and February and a winter dry season between May and August (Willems *et al*., 2009; Ayers *et al*., 2020).

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 (636 m above sea level), 18 km west of Thohoyandou town in the north-eastern part of Limpopo Province (Figure 3). The size of the study area is about 647 ha and characterized by a matrix of agricultural farms which cultivate avocado, banana, guava, litchis, macadamia (*Macadamia integrifolia*), mango, pineapples (*Ananas comosus*), and vegetables (Figure 3). Regarding cropping, the area is dominated by macadamia (128 ha; 20%), followed by mango (44 ha; 7%), banana (43 ha; 7%), guava (15 ha; 2%), litchi (13 ha; 2%), avocado (7 ha; 1%), vegetable (6 ha; 1%), pineapple (2 ha; 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 13 ha of litchis in the study area produces an annual litchi yield of about 5 tons. Around 94.26 ha (15%) of the study area is characterized by natural vegetation, which includes wild fruit trees such as fig species, forest fever tree (*Anthocleista grandiflora*), water berry (*Syzygium cordatum*), quinine tree (*Rauvolfia caffra*), coastal golden-leaf (*Bridelia micrantha*) and alien exotics like syringa berry. The study area receives an annual summer rainfall of 1356 mm during the wet summer season between the months of November and April (Tshililo *et al.*, 2021).

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).

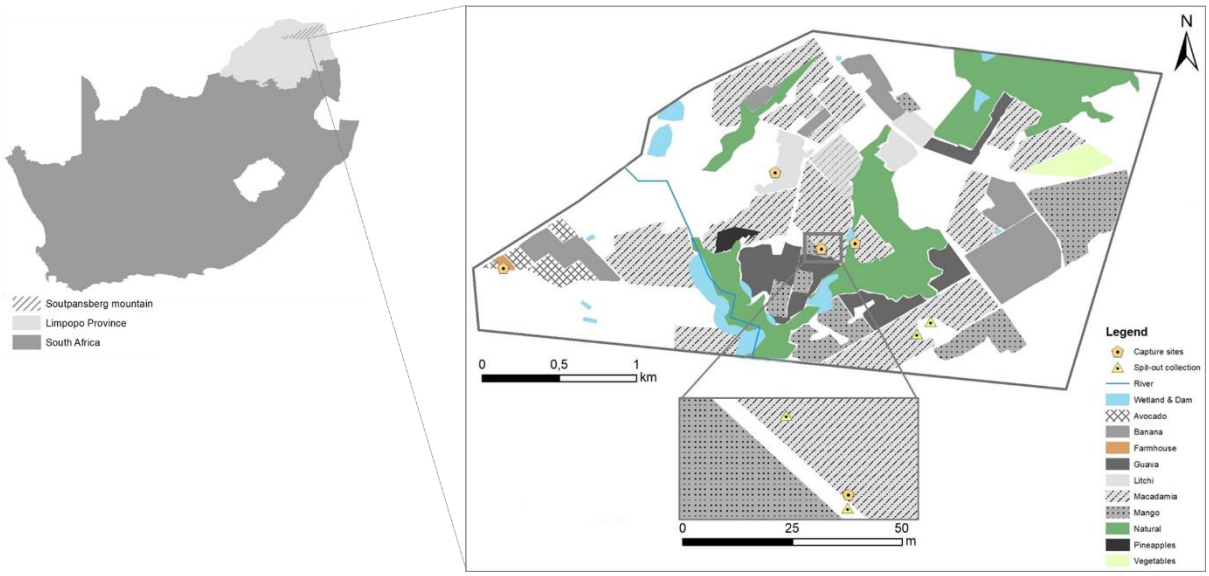


Figure 3 Map showing different land uses, localities of fruit bat captures and spit-outs collection at Farm Laatsgevonden and the surrounding farms. The white patches are abandoned farms due to land claims, which were used to cultivate guava, mango, and banana fruits.

2.2 Fruit bat capture and roost identification

Fruit bats were trapped in two study areas (Figure 2 and 3) 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 3); and in natural areas (Kutetsha Research Camp and Goro Game Reserve, Figure 2b). 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 A). Fruit bats were trapped using mist nets (12m, 9m, 3m) which were placed along pathways in natural habitats (Kutetsha Research Camp and Goro Nature Reserve) and litchi orchards (Figure 3). Nets were deployed at sunset and closed after 4 hours during litchi pre-fruiting season (March-September) and 6 hours 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 five minutes and captured bats were

immediately placed in soft cotton bags for a maximum of 2-3 hours 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 guava and litchi 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 bat evidence such as spit outs, roosts, and foraging activity (Appendix A).

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.

2.3 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`s epauletted fruit bat, Wahlberg`s epauletted fruit bat and Egyptian fruit bat), 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 bat or Peters`s epauletted fruit bat). 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 hours. When dry, seeds from faeces and spit outs were sorted by colour and size and stored in plastic Ziplock bags to avoid development of mould, noting the date of collection, GPS coordinates, and species name and sex. To collect spit outs, we searched up to 30 minutes 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, and 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 area. Faecal samples were examined after being rehydrated and sorted by using a sieve (sieve mesh diameter < 1mm) 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 (seeds and pulp) of each sample was identified. Regular seeds and spit out seeds were kept for a maximum of six days prior to sowing (Baskin and Baskin, 2014).

2.4 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 (Steinbrecher and 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 < 1mm) to extract small stones, grass, and other plant/weed seed 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 fig spp. (*Ficus* spp.), water berry (*Syzygium cordatum*), and quinine tree (*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 sterilized in order to resemble seedling growth under natural conditions. Over one and a half trays (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 their diameter of soil around them, and to push the seeds in the soil, the holes were dug 1.5 times deeper than the longest side of the seed (Baskin and Baskin, 2014).

Five fig spp. seeds were planted per cell/hole (Serio-Silva and Rico-Gray, 2002), two for water berry and one for quinine tree. The pots were monitored daily and watered whenever necessary when the soil felt dry respectively. 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 and Callihan, 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 berry and an unidentified species were excluded from the analysis due to their spit outs completely failing to germinate.

2.5 Fruit bat habitat use

A total of four fruit bats were collared with rechargeable MUSTELLA-60 GPS SRD collars, weighing a total of 6g (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 minutes from 18:00 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 30-50 m. The base station was mounted on a 3m 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 (Appendix C and E). However, the logger produced five nights of GPS data, and an average 9.6 points per night. From the three Peters`s 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.

2.6 Data analysis – diet, 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 in natural areas (Chao *et al*., 2016). This package computes the estimated diversities for standardized 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 plot 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 D), 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 D).

We used Generalised Linear Mixed-Effects Models (GLMMs) to investigate the effect of fruit bat seed spit outs on the probability of germination (binomial) and germination latency (Gaussian) in fig spp. (Crawley, 2007). GLMM's 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 and Moussalli, 2010) and likelihood ratio tests (Lewis *et al*., 2011). GLMM's were fitted in R version 3.5.1. (R Development Core Team 2008) using the lme4 package (Bates *et al*., 2015). Since there was not enough data to run the GLMM model for quinine tree, 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`s epauletted fruit bats and 28 Wahlberg`s epauletted fruit bats were caught. Only four Egyptian fruit bats were caught in the mist nets, and did not yield any spit outs nor faecal matter, nor were any active cave roost found during our study. As a result, this species could not provide any seeds to be used for the germination trials (Appendix B). A suspected Egyptian fruit bats cave roost (Mangwele cave) in Tshakhuma was vandalized and showed no sign of fruit bats when we visited it during our study. Five fruits 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 caught during the litchi ripe season.

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	*R. aegyptiacus*	*E. crypturus*	*E. wahlbergi*
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

3.2 Fruit bat diet

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 matter	Number of spit outs	Total

Epomophorous crypturus	12	2	14
Epomophorous wahlbergi	22	5	27
Epauletted fruit bats	1	20	21
		Total	62

We identified six species of wild indigenous fruits and one alien exotic fruit species in the diet of fruit bats during our study (Figure 4). Fruit bat diet revealed that bats fed mostly on wild *Ficus* spp., forest fever tree and alien exotic fruits of the syringa berry tree (Figure 4). Dietary composition showed that bats fed mostly on wild *Ficus* spp., and forest fever trees during ripe litchi season (Figure 4a). However, we found evidence of spit outs of *Ficus* spp., alien exotic fruits of syringa berry and guava in the vicinity of litchi orchards in Levubu during pre-ripe litchi season. Moreover, dietary assessment revealed that fig spp., syringa berry, forest fever tree, and coastal golden leaf dominated the bat diet in litchi orchards (Figure 4b).

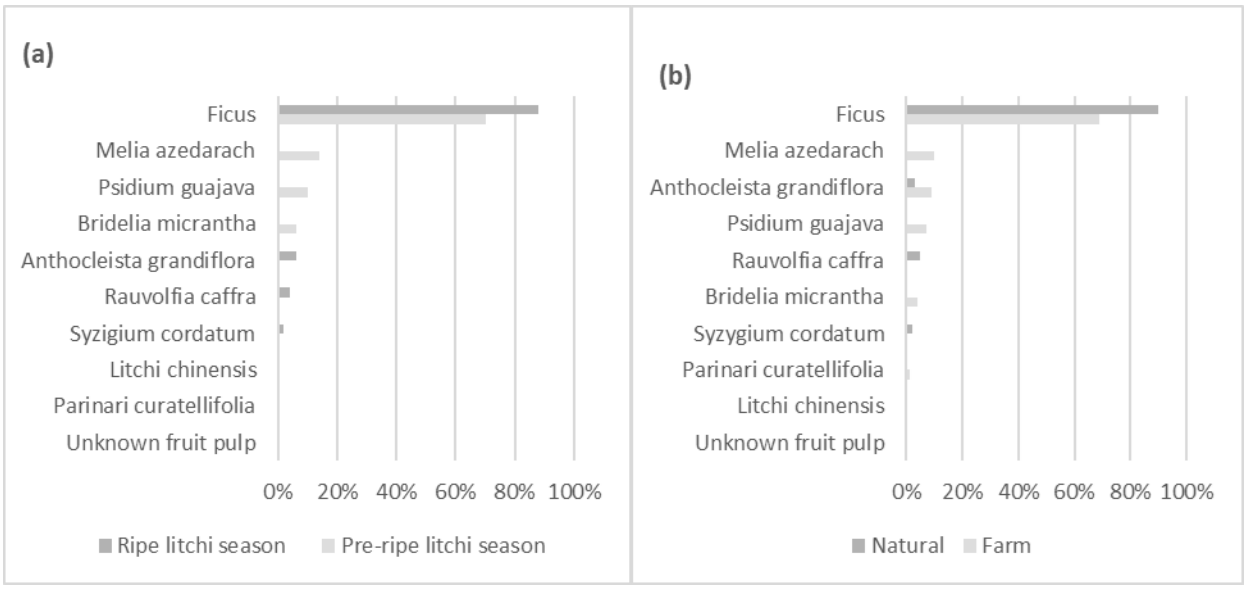


Figure 4 Diet of fruit bats expressed as percentage of faecal samples and spit outs containing fruit seeds and pulp collected from faeces, mouth, and as spit outs of *Epomophorous* spp. (*E. crypturus* and *E. wahlbergi* combined) during (a) the two litchi seasons (dark grey colour – ripe litchi (harvest) 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).

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 tree, 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 5). *Ficus* spp. have shown germination success of 18% for RS and 10% for SO, and quinine tree, 50% for RS and 28% for SO (Figure 5).

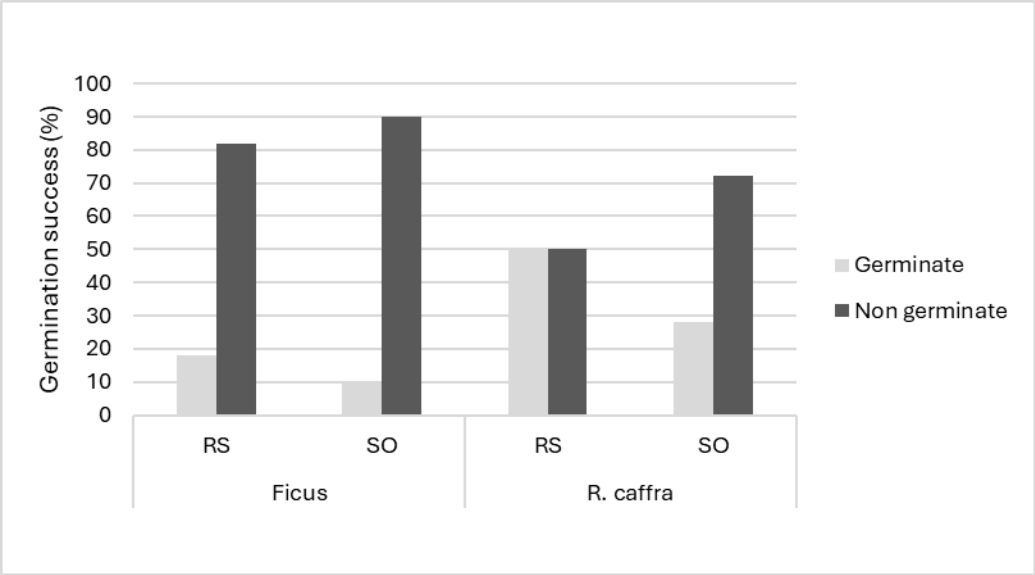


Figure 5 Germination success between treatment (RS - regular seeds; SO - spit out seeds) of *Ficus* spp. and *Rauvolfia caffra* for epauletted fruit bats (*E. wahlbergi* and *E. crypturus*). Germination success was measured as the total number of germinated seeds (seeds that managed to sprout during the germination trial) of either SO or RS divided by the total number of SO or RS, multiplied by 100.

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, x2 = 12.905, $p < 0.001$) germination probability than SR (Figure 6a). 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, x2 = 4.373, p = 0.036) germination latency than RS (Figure 6b).

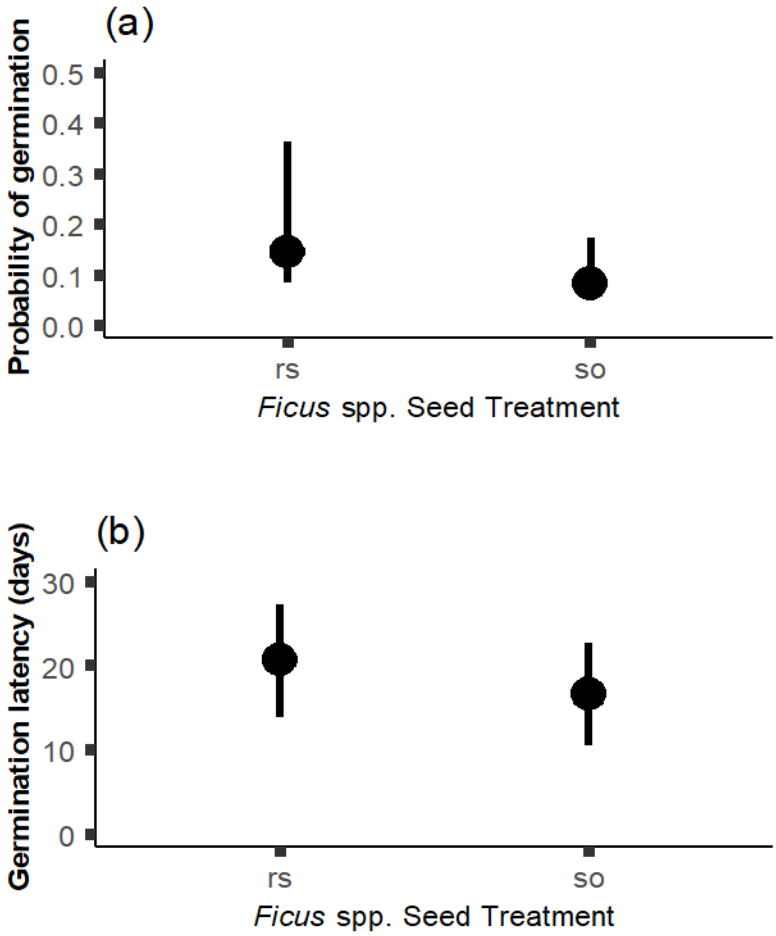


Figure 6 (a) Probability of germination (measured as the probability of germination) of bat-dispersed fruit species` seeds subject to different processing treatments (rs - regular seeds; so - spit out seeds), and (b) Germination latency (measured as the time taken by first seed to germinate after the 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). The dots show median (across the dot), and 1st (top dot) and 3rd (bottom dot) quartiles, while whiskers show the total range.

For quinine tree there was not a significant difference on germination latency between treatments (SO and RS) (df = 1, x2 = 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 tree also showed no statistically significant difference between treatments in the height at cut off day (day 30) (df = 1, x2 = 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 was 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 season and did not include/fly over ripe litchi situated about 250m away (Appendix E). 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 berry, quinine tree, mobola plum, forest fever tree and alien exotic fruit species such as syringa berry and guava were identified by direct observation (Appendix E). *Ficus* spp., quinine tree and forest fever tree 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 in 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 tree, coastal golden leaf, mobola plum, quinine tree, and water berry. Previous studies support this finding in that epauletted fruit bats show a preference for wild fruits and particularly figs (Bonaccorso *et al*., 2014; Arumoogum *et al*., 2019; 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 and Downs, 2021). Seed dispersal by fruit bats plays an important role in forest plant community maintenance and regeneration (Bortolamiol *et al*., 2014; 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 therefore facilitate the dispersion of a keystone species (*Ficus* spp.) which is also an important natural food resource for bats and other frugivores (Pothasin *et al*., 2014). Previous studies (Adams and Snode, 2013; Bonaccorso *et al*., 2014) conducted in the Kruger National Park documented that epauletted fruit bats prefer to feed on large quantities of ripe figs whose seeds pass through their gastrointestinal tracts undamaged and enhanced after being transported large distances from the feeding sites further supporting the notion that fruit bats may be important dispersers of indigenous plant species.

In contradiction to our findings for epauletted fruit bats, Egyptian fruit bats was reported to target litchi orchards during the ripe litchi season in South Africa and Mauritius (Jacobsen and du Plessis,

1976; Fleming *et al*., 2009; Tollington *et al*., 2019). Epauletted fruit bats did not seem to use ripe litchi orchards for foraging in our study, this could be because of their preference for wild fruits such as sycamore fig (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 bat 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 tree (Figure 5). These results conflict with findings by previous studies on epauletted fruit bats (Peters`s epauletted fruit bat and Wahlberg`s epauletted fruit) on seed germination of sycamore fig which reported that seeds from SO tend to germinate more successfully than RS (Snode, 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 from SOs (Snode, 2010). Our study also demonstrated that although fewer numbers of *Ficus* spp. SOs 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 Madagascan rousette bats. Given their potential to disperse a large number of *Ficus* spp. seeds as SO and improve their germination latency, epauletted fruit bats could aid habitat restoration of degraded landscapes. Our study confirms that fruit bats in our study area provide an important ecosystem service via seed dispersal providing 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 at cut off day for quinine tree. 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 (Snode, 2010, Andrianaivoarivelo *et al*., 2011; de Carvalho-Ricardo *et al*., 2014). 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 fertilizer 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 bat spent most of its time foraging over natural habitats and did not include litchi orchards during the litchi harvest season (Appendix E). This result contrasts with those of previous studies which documented that fruit bats (such as Egyptian rousette and Mauritius fruit bat) raid litchi orchards during litchi harvest season (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986; Tollington *et al*., 2019). Similarly, fruit bats were perceived to raid litchi orchards in Pakistan, resulting in fruit contamination and damage (Attaullah *et al*., 2022). The tracked Wahlberg`s epauletted fruit bat 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 a previous study where Wahlberg`s epauletted fruit bat concentrated its activity within 400m of a ripe sycamore fig (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 evidence that a need for the conservation of these species (epauletted fruit bats) is crucial for the maintenance of indigenous plant community (*Ficus*. spp).

Our dietary assessment as well as camera trapping surveys (Chapter 3) provide enough evidence that the two epauletted fruit bat species (*Epomophorous*) in Levubu do not raid litchi orchards. Perhaps,

there is a difference between 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 may 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 E). 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 less than 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 (Rollinson *et al*., 2013; Bonaccorso *et al*., 2014) 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).

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. http://dx.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

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. doi: 10.1515/mamm.2010.071

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. doi:10.3354/esr00441

ARUMOOGUM, 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

ATTAULLAH., 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 (43). https://doi.org/10.1186/s13002-022-00541-9

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). doi:10.1111/jzo.12747

AZIZ, S. A., MCCONKEY, K. R., TANALGO, K., SRITONGCHUAY, 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. *Front. Ecol. Evol*, 9. doi: 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*, 377-426. doi: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.). Academic Press, San Diego, CA, pp. 5–35

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. *J. Stat. Software*, 67, 1–48. https://doi.org/10.18637/jss.v067.i01

BOLKER, B. M., BROOKS, M. E., CLARK, C. J., et al. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol*, 24, 127–135. https:// doi.org/10.1016/j.tree.2008.10.008

BORTOLAMIOL, S., COHEN, M., POTTS, K., PENNEC, F, RWABURINDORE, P., KASENENE, J, et al. (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. doi:10.1371/journal.pone.0102177

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. doi:10.3161/150811014X683255

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. doi:10.1111/1440-1703.12102

CRAWLEY, M. J. (2007). The R Book. *Wiley*, 13, 978-0-470-51024-7. doi:10.1007/s00362-008-0118-3

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. doi:10.4404/hystrix-27.1-11722

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. doi: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. doi:10.1093/aob/mcp197, available online at www.aob.oxfordjournals.org

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. (2019). Indigenous vascular plants of the Soutpansberg, South Africa. *Bothalia – African Biodiversity & Conservation*. doi:10.4102/abc.v49i1.2402

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

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 TORREZ, E. B., BAUER, D., LOBOVA, T. & FLEMING, T. H. (2011). Ecosystem services provided by bats. *New York Academy of Science*, 1223, 1-38. doi: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//dpi.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. doi: 10.3390/molecules23051084

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*, Johannesburg, South Africa. https//dx.doi.org10.18772/22020085829

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*, 00, 1-12. https://doi.org/10.1111/aje.13132

MUCINA, L. & RUTHERFORD, M. C. (2006). The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19 South African National Biodiversity Institute, Pretoria, South Africa.

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), 474-81. 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. doi: 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. doi: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

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. http://dx.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

R CORE TEAM. (2018). R: A Language and Environment for Statistical Computing.

RELOX, R., FLORECE, L. M., BARIL, J. A. & COLADILLA, J. (2014). Assessment of fruit bats and its food preferences in Mt. Apo National Park, Kidapawan City, North Cotabato, Philippines. *Journal of Environmental Sciences and Management*, 17(1), 12-20. doi: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. doi: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*, Oxford 20, 58-66. doi: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. doi: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-serviced plant assemblage and that used by humans, *Biol. Conserv*, 174, 111–119. doi: 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. *Biotropical*, 45 (4). doi: 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 Sci. Res*, 22, 145–159. https://doi.org/10.1017/S0960258512000025

SNODE, 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

STEINBRECHER, T. & LEUBNER-METZGER, G. (2018). Tissue and cellular mechanics of seeds. *Current opinion in genetics & development*, 51, 1-10. doi: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. *Behav. Ecol Sociobiol*, 65, 13-21. doi: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* (London), 263, 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. doi: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. doi:10.17159/was/2021.v47.i4.3677

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 sacculents. *Umdaus Press*, Pretoria.

VOIGT, C. C., KELMY, D. H., BRADLEY, B. J. & ORTMANN, S. (2009). Dietary analysis of plant-visiting bats. In: Kunz, T.H., Parsons, S, eds. *Ecological and behavioral methods for the study of bats*, Baltimore, M.D: Johns Hopkins University Press. 593-609.

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. *Behav. Ecol*, 20, 985-99.

Chapter 3: Assessing litchi crop raiding activity, and species richness of fruit bats (*Epomophorus wahlbergi, Epomophorus crypturus,* and *Rousettus aegyptiacus)* in the subtropical fruit growing area of Levubu, South Africa

Vusani Mphethe[1,2], Sina Weier[2,3], Birthe Linden[2,4], Lourens Swanepoel[1,2], Daniel Parker[5] and Peter Taylor[2,3].

[1]Department of Biological Sciences, Faculty of Science, Engineering, and Agriculture, Thohoyandou, 0950, South Africa

[2]SARChI Chair on Biodiversity Value and Change, Faculty of Science, Engineering, and Agriculture, Private Bag X5050, Thohoyandou, 0950, South Africa

[3]Department of Zoology & Entomology & Afromontane Research Unit, University of the Free State, QwaQwa Campus, Private Bag X13, Phuthaditjhaba, 9866, South Africa

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

[5]School of Biology and Environmental Sciences, University of Mpumalanga, Mbombela, 1200, South Africa

Prepared for: Acta Chiropterologica

Abstract

Fruit bat farmer conflict is experienced by both commercial and small-scale farming communities and requires attention for the conservation of fruit bats. This conflict often stems from perceived and actual damage to crops by fruit bats. However, the crop-raiding impact of fruit bats, with other species remains unexplored. In this study, we conducted a camera trap study to determine the species richness of both crop raiders and incidentally observed species in litchi (*Litchi chinensis*) orchards, Levubu, South Africa. We tested the hypothesis that the litchi harvest season would have higher species richness of crop raider species (due to the abundance of ripe litchi fruits) and incidental species (due to insect abundance e.g., Long-tailed paradise whydah) than the litchi pre-harvest. We also predicted that the number of crop-raiding bat species (*Epomophorus wahlbergi, Epomophorus crypturus,* and *Rousettus aegyptiacus*) would be higher compared to non-crop raiding species. We further predicted that we would record the highest activity of crop raiders such as *E. wahlbergi, E. crypturus,* and *R. aegyptiacus* during the litchi harvest season/litchi ripe season (December), compared to the litchi pre-harvest season/litchi pre-ripe season (October/November). We found that the litchi harvest season had significantly higher species richness than the litchi pre-harvest season. However, crop raider species richness (including bats) was lower, compared to non-crop raider species (e.g. common duiker) during the harvest season. In terms of activity, we found that fruit bats (unidentified fruit bats) had lower activity (RAI of 2.49) compared to Dark-capped Bulbuls (*Pycnonotus tricolor*; RAI of 43.44). Fruit bats did not show any change in seasonal activity during the litchi pre-ripe and ripe seasons. Interestingly, we did not record any fruit-raiding behavior by fruit bats (*E. wahlbergi, E. crypturus,* and *R. aegyptiacus*). Our results suggest that fruit bats in our study area do not respond to litchi fruit abundance in contrast to what farmers believe, and that fruit bat crop raiding might be elsewhere.

Keywords: Agroecosystems, activity patterns, litchis, camera trap

1. Introduction

Human-wildlife conflict is one of the main threats to the survival of many species worldwide (Mekonen, 2020). Importantly, developing countries have been reported to be more vulnerable to such conflict than developed nations (Fairet and Magu, 2012), due to more rapid growth in human populations, and expansion of settlement into wildlife habitats (Kate, 2012). Human-wildlife conflict is experienced by both small-scale and commercial farmers in agricultural regions where human populations have expanded into animal territory (Ladan, 2014). Crop raiding activity by different animal species in agricultural landscapes is a global problem, especially during harvest season (Jacobsen *et al*., 1986; Gobosho *et al*., 2015; Tollington *et al*., 2019). Fruit bats have been reported to cause significant economic damage to commercially cultivated crops in agroecosystems (Aziz *et al*., 2016).

Crop-raiding fruit bats are often killed in retaliation for crop losses in different parts of the globe (Fujita and Tuttle, 1991; Adams and Pedersen, 2013). For example, in Australia *Pteropus* spp. were reported by farmers as" black devils" which can destroy an entire crop in a few nights (Adams and Pedersen, 2013). Similarly, *Pteropus* spp. were perceived to prevent fruit set on Durian kampong (*Durio zibethinus*), whose flowers rely mostly on bats for pollination (Bumrungsri *et al*., 2009). GPS-tracked Lyle`s flying fox (*Pteropus lylei*) was reported to target mango (*Mangifera indica*), banana (*Musa* spp.), and pawpaw (*Carica papaya*) orchards in central Thailand (Weber *et al*., 2015). While in Turkey, the Egyptian fruit bat (*Rousettus aegyptiacus*) was documented to raid citrus (*Citrus* spp.) plantations (Albayrak *et al*., 2008). Mauritian flying fox (*Pteropus niger*) was shown to cause 42% of the damage on litchi crops in Mauritius (Tollington *et al*., 2019). Commercial fruits like avocado (*Persea americana*), guava (*Psidium guajava*), and common grape vine (*Vitis vinifera*) were also targeted by fruit bats (Srinivasulu and Srinivasulu, 2002; Vincenot *et al*., 2015; Oleksy *et al*., 2015). It thus appears that fruit bats are among the worst pests in agroecosystems resulting in severe crop loss and significant economic hardship.

However, crop raiding is not unique among fruit bats, and many other species raid crops such as Olive baboon (*Papioanubis*), Bush pig (*Potamochoerus larvatus*), common Warthog (*Phacochoerus africanus*), Grivet monkey (*Cercopithecus aethiops*) and crested porcupine (*Hystrix cristata*); (Gobosho *et al*., 2015). Similarly, African bush elephant (*Loxodonta africana*) was documented to account for 80-90% of crop damage in Ghana (Parker *et al*., 2007), with a total of 500 households losing 70% of their food crops to elephant activity (Barnes *et al*., 2003). Similarly, Weaver birds

(*Ploceidae*) was reported to cause crop damage problems in the Tiko farming area of Cameroon (Maurice *et al*., 2019). In Levubu, South Africa Vervet monkey (*Chlorocebus pygerythrus*) was also responsible for the damage to macadamia orchards (Linden *et al*., 2019). As such, exploring the fruit-raiding activity of fruit bats should be done in combination with other potential crop-raiding species in the same crop.

Litchi (*Litchi chinensis*) belongs to the family Sapindaceae and a commercially important fruit cultivated in the subtropical regions of South Africa (Froneman, 2010). The South African litchi industry produced 5545 tons of litchis during the 2017/2018 season, of which 65% of the litchi produced are exported, 24% sold to the local market, and 11% processed into products (Haraji *et al*., 2020). South Africa`s litchi production contributes more than $6 869 795 annually towards the country`s gross domestic product (GDP), resulting in job creation in the agricultural and food processing sectors (DAFF, 2015). The litchi industry in South Africa is subjected to pest insects such as fruit flies (*Ceratitis* spp.), Litchi moth (*Cryptophlebia peltastica*), False codling moth (*Thaumatotibia leucotreta*), and fruit bats (*R. aegyptiacus*) which are known to cause significant economic damage to the litchi crop (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986; Grove *et al*., 2014; Tollington *et al*., 2019). Similarly, birds such as Dark-capped bulbul (*Pycnonotus tricolor*), Speckled mousebird (*Colius striatus*), and primates like C. *pygerythrus* also raid litchi orchards thereby causing significant economic damage (Barrett, 2004; Olesky *et al*., 2018).

Camera trapping is an important tool and is commonly used in the assessment of wildlife abundance, composition, density, distribution, population trends, and behavior (Burton *et al*., 2015). Camera traps are useful to facilitate the monitoring of a variety of species (De Bondi *et al*., 2010) over large spatial and temporal scales as well as across multiple environments (Rovero *et al*., 2013; Meek *et al*., 2014; Steenweg *et al*., 2016). These traps could be programmed to detect animal movement (Welbourne *et al*. 2016), or time-triggered images (Smith *et al*., 2020). Camera trapping has shown the potential to collect vital information on animal activity patterns as well as foraging behavior (Cutler and Swann, 1999; De Bondi *et al*., 2010).

This study forms part of a larger study that quantified crop raider damage on litchi trees, using vertebrate exclusion experiments. In this study, we aimed to provide insight into crop raiding species and their activity patterns in response to ripe litchi fruit abundance using a camera trap experiment on two litchi farms over two years. We hypothesized that the litchi harvest season (during austral summer) would have the highest activity of crop-raiding bats (*E. wahlbergi, E. crypturus,* and *R.*

aegyptiacus). We predicted that litchi crop abundance would have a positive influence on the species richness of crop raiders and other animals (incidentally recorded) within the same orchards and between orchards. We further predicted that crop raider species richness (due to the availability of ripe litchi fruit in summer) would be higher than non-crop raider species (because of insect abundance attracted by the rotting/cracked litchi fruits) recorded at the ground and canopy level in response to the abundance of ripe litchi fruits. Wild animals have been documented to spend more time in agricultural orchards with abundant food sources (Taylor *et al*., 2013; Gobosho, 2015; Tollington *et al*., 2019). Thus, we also predicted that crop raider fruit bat species (*E. wahlbergi, E. crypturus,* and *R. aegyptiacus*) would spend more time foraging over ripe litchi orchards during December months when the fruits are ripe, compared to October and November when the fruits are not yet ripe. Other suspected crop raiders would likely include *P. tricolor*, *C. striatus,* and *C. pygerythrus* (Jacobsen *et al*., 1986; Olesky *et al*., 2018; Tollington *et al*., 2019).

2. Materials and methods

2.1 Study area

2.1.1 Litchi production in South Africa

Litchi chinensis have been cultivated in South Africa for the past 146 years, with the first trees imported from Mauritius, and a total of 10 444 tons were produced during the 2016/2017 production season in South Africa (DAFF, 2018). Litchi crop is mainly grown in the Limpopo and Mpumalanga provinces, with KwaZulu-Natal being another producer of litchi crops in South Africa. The estimated total area that accounts for litchi production in South Africa is 1 731 ha (Begemann, 2014). In the Limpopo province of South Africa, litchi fruit is mostly produced in areas like Trichardtsdal, Tzaneen, Makhado (Louis Trichardt), and Levubu. Around 38% of litchi in South Africa is produced in the Limpopo province, with Tzaneen being a major producer of litchi crops (DAFF, 2018). The litchi season in South Africa begins during mid-October in Mpumalanga (Malelane and Komatipoort), peaks in December, and ends around late-February in areas such as Levubu, Louis Trichardt, Tzaneen, and Nelspruit (Froneman, 2010; DAFF, 2018).

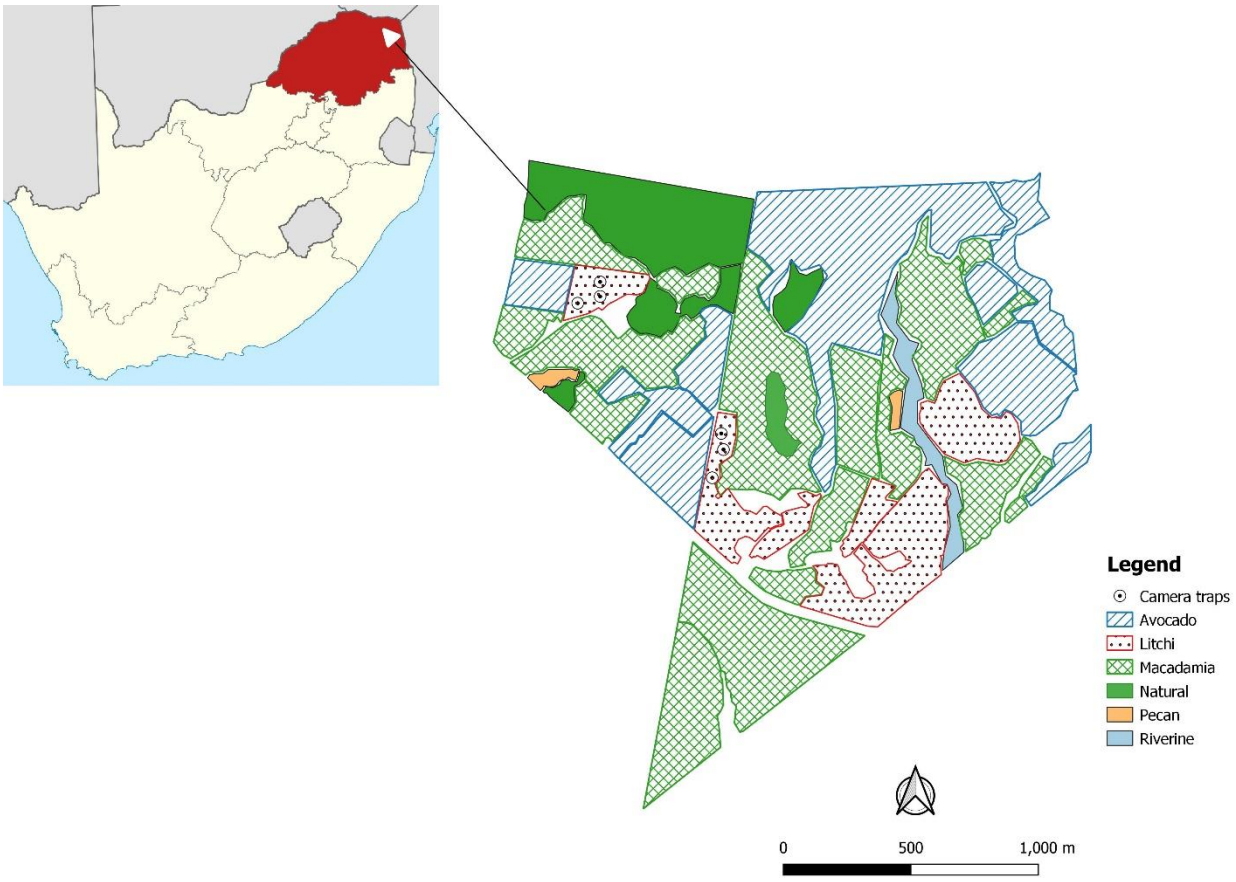


Figure 7 Map showing the study area, camera traps location, and major habitat types of the two farms situated in the Levubu subtropical crop growing area, South Africa.

2.1.2 Neuhoff Farm (Fritz Ahrens Boerdery)

The first orchard used as a study area was situated on Neuhoff Farm (-23.06588879S, 30.0783689E), located on the foothills of the Soutpansberg mountain range (855 m above sea level), about 20 km east of Louis Trichardt (Figure 7). The size of the study site is about 183 ha and characterized by litchi (*L. chinensis*), macadamia (*Macadamia integrifolia*), avocado (*P. americana*), and pecan (*C. illinoinensis*) orchards. The area is dominated by *M. integrifolia* (47.10 ha; 25.74%), followed by *P. americana* (16.69 ha; 9.12%), *L. chinensis* (2.47 ha; 1.35%), and *C. illinoinensis* (1.20 ha; 0.66%). The natural vegetation (29.5%) of the study farm mostly covers the Soutpansberg mountain. Neuhoff Farm produces an annual total yield of 83 tons of litchis during the harvest season. The area receives an annual summer rainfall of between 930 mm and 960 mm, mostly between November and April (Taylor *et al.*, 2013).

2.1.3 Rionde Fruit Farm (Gilbert Packer)

Our second study site was situated in Rionde Fruit Farm (-23.0722691S, 30.08265997E), neighbouring Neuhoff Farm (Figure 7) and located on the foothills of the Soutpansberg mountain range (888 m above sea level). The size of this study site is about 240 ha and characterized by *L. chinensis*, *M. integrifolia*, and *P. americana* orchards. In terms of cropping, the study site is dominated by *M. integrifolia* (90 ha; 37.50%), followed by *P. americana* (50 ha; 20.83%) and *L. chinensis* (33 ha; 13.75%). Rionde Fruit Farm produces an annual litchi yield of 250 tons during the harvest season. The study site receives similar annual rainfall as Neuhoff Farm.

2.2 Experimental design

Our camera trap survey on crop-raiding animals forms part of a larger study on the impact of crop raiding on litchi trees. Experiments were conducted on the two commercial litchi farms (Figure 7). The experimental exclusion took place over two consecutive litchi harvest seasons, during the years 2019 and 2020. A total of 6 cages were constructed, each enclosing one litchi tree with a nylon mesh net (mesh size of 2×3 cm in size) that only allows arthropods or small animals (e.g., ants, moth) to enter but excludes flying vertebrates (bats and bird), monkeys and large herbivores (Figure 8). We applied two treatments on our two study sites, the “FULL” exclosure which was closed all times (to prevent bats, birds, and monkeys to access the tree), and the “CONTROL” (open at all times and without frames or nets). Each treatment was paired with an adjacent plot (CONTROL) of the same area as the cage (FULL) marked with a taper (danger tape) and resulted in three paired treatments on each farm. At ground level, we deployed one motion-activated camera to monitor ground-level animals (Figure 8). The camera trap experimental setup resulted in 6 camera traps monitoring tree tops (3 per farm, by 2 farms) and 4 cameras on ground level (2 per farm) of the “CONTROL” treatment. The canopy camera traps were programmed to take pictures every 5 minutes (during early 2019), and 1 minute during late 2019 and throughout the 2020 sampling periods (litchi pre-harvest and harvest season). The canopy camera traps were time triggered since bats, birds, and insects are small and fast in movement and might not trigger the motion sensor of the camera, resulting in missed detections (Wellington *et al*., 2014). Ground-level camera traps were motion triggered since the animals targeted (monkeys)were larger and slow enough to trigger the motion sensor in the camera trap (Meek *et al*., 2015). However, farmers in our study area use monkey guards to deter vervet monkeys from entering the litchi orchards. The cameras were deployed during two sessions,

immediately after the first litchi fruit set to cover pre-harvest (pre-harvest session: October - November) and litchi harvest season (harvest session: December - January). The canopy camera traps were deployed for 203 days, and ground camera traps for 262 days, resulting in a total of 465 days at Neuhoff Farm. At Rionde Fruit Farm, canopy camera traps were deployed for 213 days, with ground cameras deployed for 206 days, adding up to a total of 419 days. A camera trap night (from sunset to sunrise) was defined following Abrams *et al.*, (2018), as each night a single camera is active for the total number of operational cameras. However, the camera trap night was used to calculate the relative abundance index (RAI) and the offset.

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

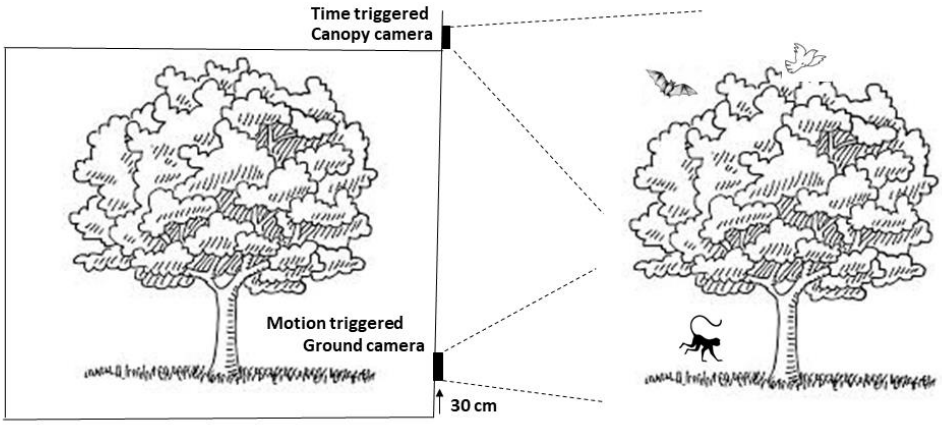


Figure 8 Camera trap setup showing time-triggered canopy level camera trap and motion-triggered ground level camera trap set up at the two study sites (litchi farms) in Levubu, South Africa.

2.3 Image processing

The images were tagged in the Digikam image software (version 5.6.0 available at www.digikam.org) and tagged information was written to the image meta-data. Birds were identified with the use of Sasol eBirds Guide App Southern Africa software (www.mydigitalearth.com) and the help of Mr. Samson Mulaudzi (professional bird guide in the Vhembe Biosphere region). Where

possible, abundance data per image detection was also recorded (abundance was defined as the number of animals present in each detection/image). The meta-data were extracted through R code for Digikam using packages RSQLite and DBI (R Development Core Team, Vienna, available at t http://www.r-project.org).

2.4 Sample completeness and species diversity

The iNEXT (INterpolation and EXTrapolation) package for R was used to determine sample completeness and species diversity from camera trap data collected during the litchi pre-harvest season and the litchi harvest season on the two litchi farms (Chao *et al*., 2016). This package computes the estimated diversities for standardized 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).

2.5 Species richness

We used Generalised Linear Mixed-Effects Models (GLMMs) to investigate the effect of litchi crop abundance on species richness (Poisson) between species diet (crop raider and incidentally observed species), and seasons (litchi harvest and litchi pre-harvest season) (Crawley, 2007). GLMMs are the preferred model of analysis for count data (Zuur *et al*., 2009) since it allows for categorical and non-normal distribution of the response variable (Bolker *et al*., 2009; Sileshi 2012). We modelled species diet treatment (crop raider and incidental observations) and season treatment (pre-harvest and harvest) as the fixed effects to evaluate the effect of litchi crop abundance on species richness. We contrasted the 'treatment' model to a null model (no effect modelled) and evaluated model parsimony with Akaike information criteria (Symonds and Moussalli, 2010) and likelihood ratio tests (Lewis *et al*., 2011). GLMMs were fitted in R version 3.5.1. (R Development Core Team 2008) using the lme4 package (Bates *et al*., 2015).

2.6 Activity pattern of crop raider

Annual variation in day length has a direct influence on wildlife activity patterns (Nouvellet *et al*., 2012), and because of this, nocturnal species were reported to forage into daylight hours during summer due to shorter nights to meet their energy requirements (Schai-Braun *et al*., 2012). However,

bat activity has been reported to correspond to food availability, especially in agricultural settings (Jacobsen *et al*., 1986; Kunz *et al*., 2011; Taylor *et al*., 2013; Tollington *et al*., 2019). To investigate the variation in crop raider activity during different litchi crop sessions/stages relative to sunrise/sunset (whether nocturnal/diurnal activity differs between different crop stages, the solar cycle historical data for 2019/2020 was obtained from Meteogram.org-South Africa), the data were grouped according to months (October, November, and December) from the time when the first fruits set until crop harvest session. Crop raiders detected between 00:00 and 11:59 were assigned an offset relative to sunrise and between 12:00 and 23:59 an offset relative to sunset. However, this followed Caravaggi *et al*., (2018) who grouped solar cycle historical data according to season (i.e., spring, summer) to determine activity relative to sunrise/sunset. Furthermore, animal detections between 00:00 and 11:59 were offset relative to sunrise, and detections between 12:00 and 23:59 were offset relative to sunrise. Diurnal period was defined as the time between 1 hour after sunrise and 1 hour before sunset, and nocturnal period as time between 1 hour before sunrise and 1 hour after sunset. To investigate the differences in offsets, we used an ANOVA and post hoc Tukey HSD tests with sunrise/sunset offset as a dependent variable and months as the explanatory variable. The daily activity patterns of the vervet monkey, Speckled mouse bird, Dark-capped bulbul, and fruit bat were estimated using the overlap package (Meredith and Ridout, 2018) in R-studio version 3.5.2 (R Development Core Team, Vienna, available at t http://www.r-project.org).

2.7 Relative abundance indices

Data obtained from camera trapping were used to estimate the relative abundance indices (RAI) of flying and non-flying species, and computed as RAI = $\left(\frac{E}{N}\right)\times 100$, where E is the total number of detections of species (independent photographs = photographs of the same species separated by a time interval of more than 30 minutes) by all cameras and N is the total number of camera trap days by all cameras throughout the study area (Jenks *et al*., 2011). Photos of each detected species were considered an independent event when the time interval between consecutive photographs of the same species was more than 30 minutes (O'Brien *et al*., 2003). Photographs were grouped in the following order, flying (i.e., bats, birds, insects) and non-flying (i.e., monkeys, genets, common duiker). To evaluate the effect of season on species RAIs, the Kruskal Wallis test was conducted, and a Welch`s t-test was performed to analyze differences in species RAIs between ground and canopy levels.

3. RESULTS

Our survey conducted at two litchi farms (Figure 7) produced a total effort of 884 camera trap nights and classified a total of 856 frames as independent photographs (Table 1). During the year 2019, two canopy camera traps at Rionde Fruit Farm malfunctioned (failed to take pictures). To increase our effort and account for lost data we left our camera traps for more nights at Neuhoff Farm, where the owner agreed to harvest his litchi in January of the following year (2020), thus we decreased the time for our canopy camera traps from 5 minutes to 1 minute to capture more data. We repeated the same experiments during the year 2020 litchi season with cameras set to record pictures every minute and managed to get complete data. From the total of 25 species recorded, four were identified as crop raiders, and 19 were incidentally observed species.

We achieved high sampling coverage, suggesting complete sampling (Figure 9b). Total species diversity was higher at Neuhoff Farm compared to Rionde Fruit Farm (Figure 9a).

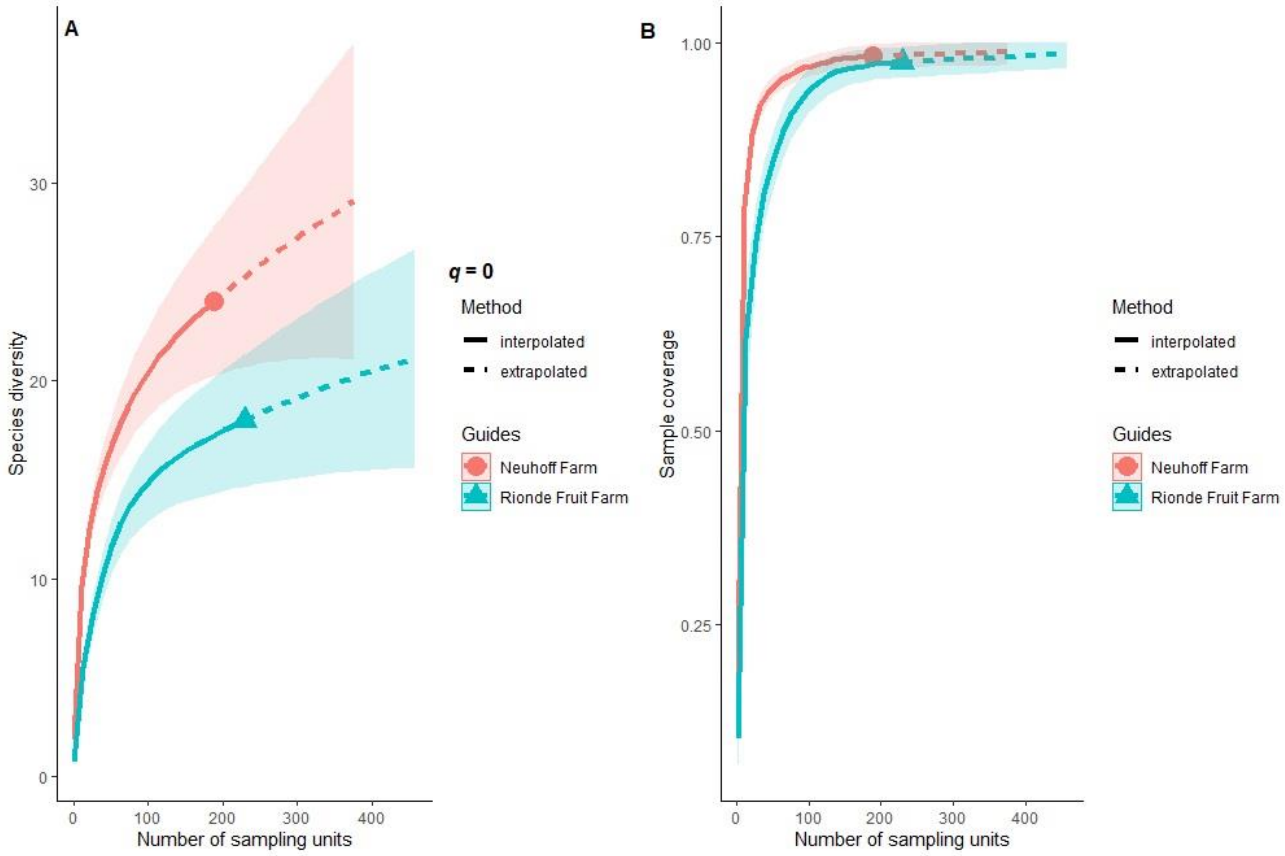


Figure 9 Sample rarefaction curves showing (A) Species diversity in terms of $q = 0$ and (B) sample completeness from camera trapping on two litchi farms in Levubu (Neuhoff Farm and Rionde Fruit

Farm), South Africa. The x-axis in figure A and B represent the number of sampling units which is the camera trap nights/days.

There was a statistically significant difference in species richness (df = 1, x^2 = 4.674, p = 0.031) between the litchi pre-harvest and the harvest season (Figure 10). However, there was not a statistical difference in species richness (df = 1, x^2 = 0, p = 0.996) between crop raider and incidental observation species.

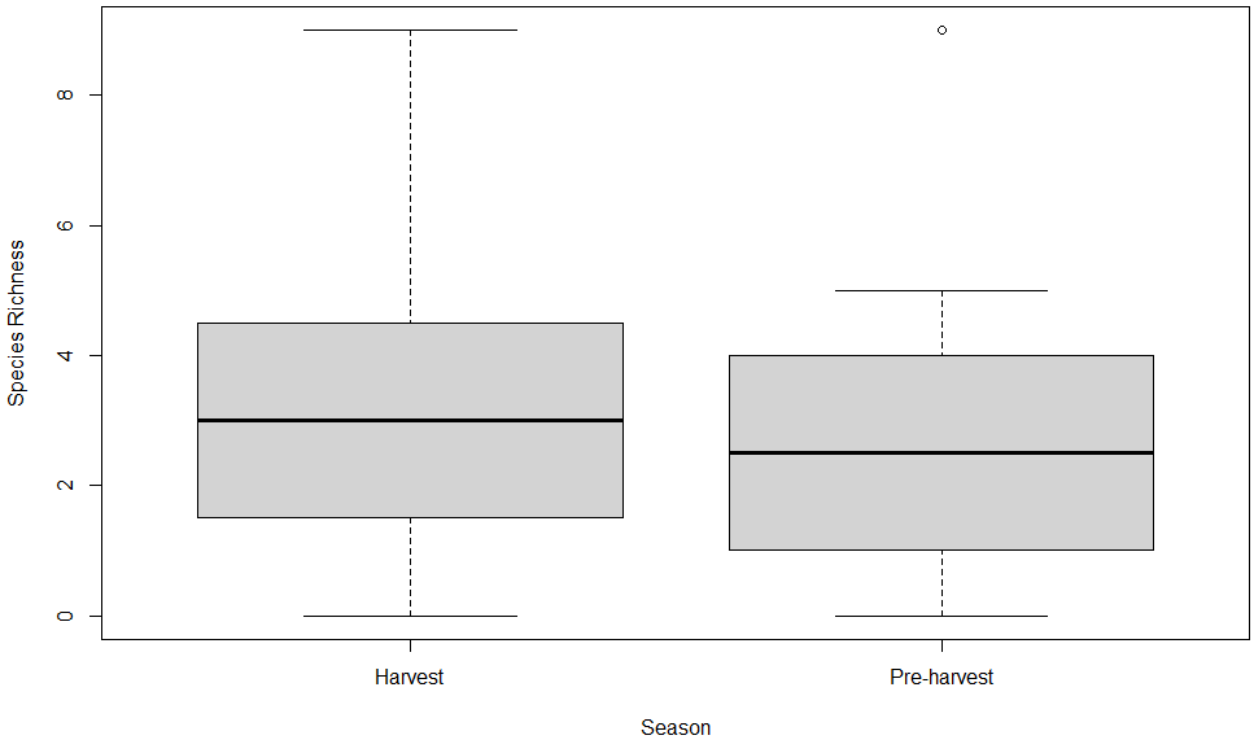


Figure 10 Species richness between litchi pre-harvest and harvest season on two litchi farms in the Levubu subtropical fruit growing area. The boxes show median (solid black line across the box), and 1st (top box) and 3rd (bottom box) quartiles. Whiskers show the total range and dots outside of the boxes indicate outliers.

The species RAIs did not differ statistically between litchi pre-harvest and harvest seasons (df = 1, x2 = 0.356, p = 0.551). There was no statistically significant difference between canopy and ground species' RAIs (t(32.5) = 0.928, p = 0.36). However, the mean RAI at the canopy level was 2.10 (SD = 5.25), whereas the mean at the ground level was 1.10 (SD = 1.77). RAIs did not differ statistically among flying and non-flying groups (t(48.9) = 0.0368, p = 0.971). The mean RAI in the flying group was 1.64 (SD = 4.67), and 1.61 (SD = 2) for the non-flying group (Table 3).

Table 3 A comparative Relative Abundance Index (RAI) of different wildlife species based on camera trap photographs in the Levubu subtropical area, Limpopo, South Africa between October 2019 to January 2020.

Photographs	Common Name	Site	Number of independent photos	RAI
Flying				
Family: Accipitridae *Polyboroides typus*	African Harrier-hawk	Ground	1	0.11
Family: Phasianidae *Coturnix coturnix*	Common Quail	Ground	1	0.11
Family: Pycnonotidae *Pycnonotus tricolor*	Dark-capped Bulbul	Canopy	384	43.44
Family: Pteropodidae	Fruit bat	Canopy	22	2.49
Family: Ploceidae *Ploceus subaureus*	Golden Weaver	Canopy	9	1.02
Family: Numididae *Numida meleagris*	Helmeted Guinea fowl	Ground	5	0.57
Family: Threskiornithidae *Bostrychia hagedash*	Hadeda Ibis	Ground	1	0.11
Family: Sphingidae	Hawk moth	Canopy	13	1.47
Suborder: Microchiroptera	Insectivorous bat	Canopy	1	0.11
Family: Viduidae *Vidua paradisaea*	Long-tailed Paradise Whydah	Canopy	29	3.39
Order: Lepidoptera	Moth	Canopy	40	4.52
Family: Ploceidae *Euplectes ardens*	Red-collared Widow	Canopy	3	0.34

Family: Coliidae *Colius striatus*	Speckled Mouse bird	Canopy	9	1.02
Class: Aves	Unidentified bird	Canopy	2	0.23
Class: Insecta	Unidentified insect	Canopy	60	6.79
Family: Ploceidae *Euplectes albonotatus*	White-winged widow bird	Canopy	3	0.34
Family: Ploceidae *Euplectes capensis*	Yellow bishop	Canopy	7	0.79
Non-flying				
Family: Felidae *Felis catus*	Domestic cat	Ground	2	0.23
Family: Bovidae *Sylvicapra grimmia*	Common duiker	Ground	96	10.86
Family: Viverridae *Genetta genetta*	Common genet	Ground	23	2.60
Family: Hominidae *Homo sapiens*	Human	Ground	80	9.05
Family: Hystricidae *Hystrix africaeaustralis*	Porcupine	Ground	27	3.05
Family: Cercopithecidae *Cercopithecus pygerythrus*	Vervet monkey	Ground/Canopy	12	1.36
Family: Suidae *Phacochoerus africanus*	Warthog	Ground	3	0.34
Family: Herpestidae *Ichneumia albicauda*	White-tailed mongoose	Ground	22	2.49

There was a significant difference between months in *P. tricolor* activity (f(2)=11.14, p < 0.001), December was significantly different from other months, due to increased activity from litchi fruit abundance. There was a significant difference in offsets between months in *C. striatus* (f(2)=6.429, p = 0.038). Pteropodidae (f(2)=2.493, p = 0.13) or *C. pygerythrus* (f(2)=0.805, p = 0.477) showed no significant difference in offsets between months.

Pycnonotus tricolor was active throughout the day and showed bimodal peaks of activities around 6:00 h and 18:00 h (Figure 11a). Pteropodidae exhibited unimodal peak of activity around 0:00 h midnight and showed diurnal activity (Figure 11b). *Colius striatus* also exhibited bimodal peaks and was active throughout the day (Figure 11c). *Chlorocebus pygerythrus* had peaks of activity around 6:00 h and 18:00 h and was less active during the hottest hours of the day (Figure 11d).

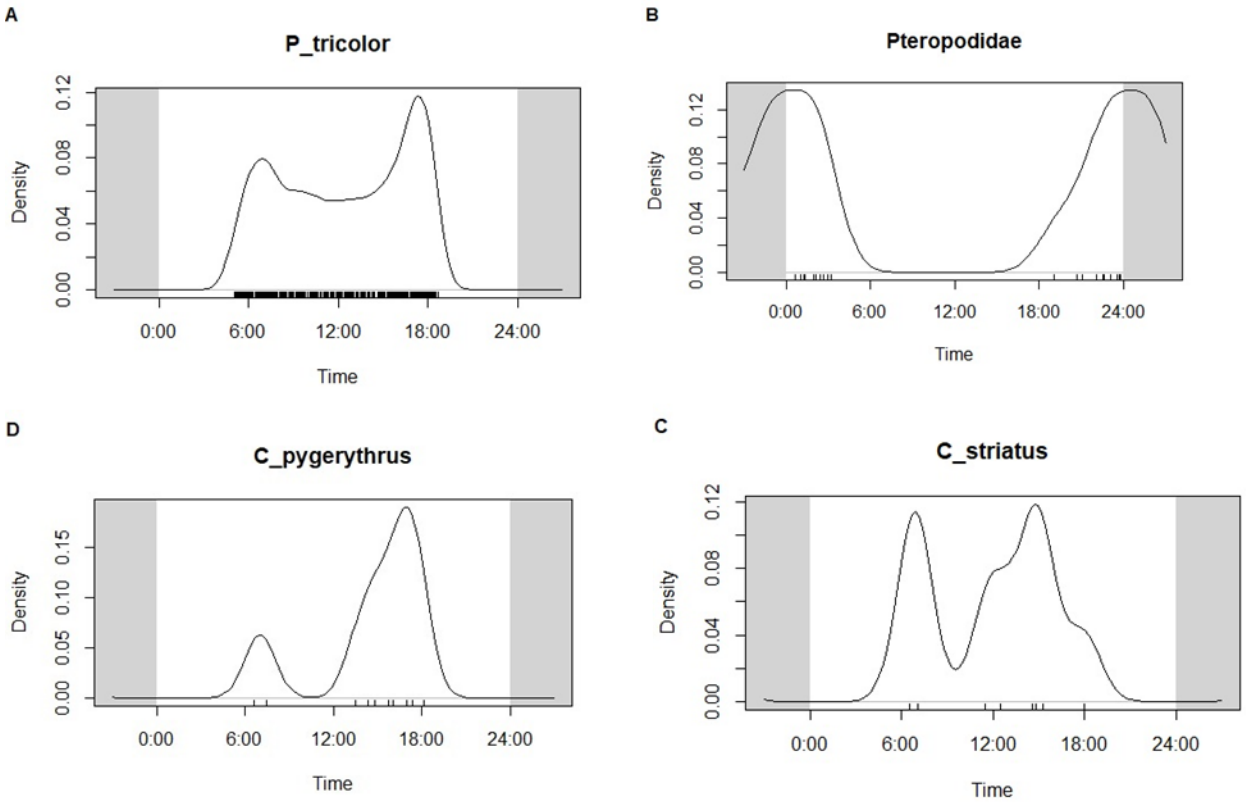


Figure 11 Kernel density plots of daily activity pattern of crop raider species between two litchi farms, Levubu subtropical area, Limpopo, South Africa.

4. Discussion

Our camera trap data produced a total of 17 flying species (including 2 unidentified) and 8 non-flying species, with our camera trap effort having likely detected all the species found in our study area. Our camera trap survey has shown that litchi fruit abundance during the harvest season (December) led to an increase in species richness of crop raiders and incidentally observed species. These findings were similar to previous studies which have documented that vertebrates including bats respond to high food abundance in agroecosystems (Cleveland *et al*., 2006; Kunz *et al*., 2011; Taylor *et al*., 2013). Jacobsen *et al*., (1986) also reported Egyptian fruit bats targeting litchi orchards during the litchi harvest season.

However, we found that high litchi fruit abundance did not increase crop raider species richness which includes fruit bat (*E. wahlbergi, E. crypturus, R. aegyptiacus*), during the harvest season, compared to incidentally observed species. This result contrasts with previous studies which documented that fruit bat species like *R. aegyptiacus* target ripe litchi orchards with high fruit abundance (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986). Pteropodidae opportunistic feeding on ripe litchi orchards was also reported in Australia, Israel, and Mauritius (Price, 2013; Aziz *et al*., 2016; Tollington *et al*., 2019). In New South Wales, commercial farmers reported suffering a significant crop loss and claim that 80% of their crop was lost to *Pteropus* spp. (Adams and Pedersen, 2013). In Mauritius, *P. niger* raids on ripe backyard litchi and mango trees caused significant damage (Tollington *et al*., 2019). Our low species richness recorded by fruit bats during the litchi harvest season could be due to fruit bats' preference for wild fruits over commercially cultivated litchi fruits. The Malagasy fruit bat (*Rousettus madagascariensis*) was also reported to feed on native fruits like the heart-leaved fig (*Ficus polita*), rose apple (*Syzygium jambos*), and malay apple (*Syzygium malaccense*) compared to commercially cultivated fruits such as *L. chinensis* due to their preference for high lipid and calcium content than fructose (Andrianaivoarivelo *et al*., 2012). However, *R. aegyptiacus* recorded a high percentage of native food items in their diet compared to commercially cultivated fruits (Korine *et al*., 1999). Furthermore, the Leschenault`s Rousette Bat (*Rousettus leschenaulitti*) diet comprised 75% of wild fruits, compared to commercially cultivated fruits (Thapa, 2021). Similarly, other previous studies also documented that fruit bats prefer to feed on wild figs fruits (Bonaccorso *et al*., 2014; Arumoogum *et al*., 2019). Moreover, although agricultural habitat dominates the landscape at our study sites, these bats can probably move up into the nearby less transformed Soutpansberg mountains, whereas in a country like Mauritius, bats might

have no other places to go and are forced to raid fruit crops. As a result, future studies should include a broader-scale landscape study combined to radiotracking of these bats to determine their actual home range.

Similarly, we found that the species richness of other crop raiders like birds (*P. tricolor, C. striatus*) and primates (*C. pygerythrus*) were lower compared to incidentally observed species. These findings are in contrast to other previous studies which documented that crop raiders such as birds and primates are opportunistic in their feeding habit and responded positively to increased ripe fruits. (Lee and Priston, 2005; Linden *et al*., 2019; Maurice *et al*., 2019). Our low species richness dominated by *P. tricolor* and *C. striatus* during the harvest season can be due to several reasons. For example, it could be due to the availability of orchard natural edges with higher diversity of fruit sources. In Central Europe, birds recorded increased species richness in natural forest habitats, compared to lower species richness in nearby agricultural habitats (Dvorakova *et al*., 2022). Olimpi *et al*., (2022) documented that increasing semi-natural habitats around farms decrease crop damage. Orchards' natural edges provide semi-natural habitats for birds and enhance ecosystem biodiversity (Mkenda *et al*., 2019). Our lower species richness recorded by *C. pygerythrus* during the litchi harvest season can be due to regular patrols by monkey guards. Findlay and Hill, (2020) recommended that to effectively control monkeys, guards should chase monkeys further away from the fruit orchards before midday. In Uganda, guarding was the most effective control measure against crop raiding by animals such as baboons, vervet monkeys, and chimpanzees (Kate, 2012). Similarly, active guarding by farmers was found an effective measure to reduce crop raiding by monkeys in Rhwanda (Mc Guinness and Taylor, 2014).

We found that Pteropodidae had low RAI, compared to *P. tricolor*, which reported the highest RAI amongst litchi crop raiders. These findings were contrary to previous studies (Kunz. *et al*., 2011; Aziz *et al*., 2016; Tollington *et al*., 2019) which documented that fruit bats cause significant economic damage to commercial litchis. Aziz *et al*., (2016) have documented that fruit bats target ripe orchards of *Mangifera indica, Asimina triloba, P. guajava, L. chinensis, Musa acuminata, Phoenix dactylifera* and cause significant economic damage. Other studies conducted in litchi orchards in South Africa have reported that *R. aegyptiacus* are the major cause of damage to litchi fruits (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986). Our lack of fruit-raiding activity by fruit bats can be due to several reasons. For example, litchi farmers have reported that *R. aegyptiacus* roosts and forages in groups, causing significant economic damage to their produce. Furthermore, *R.*

aegyptiacus do not seem to be abundant in Levubu (Mphethe *et al*., 2023), perhaps this could explain the lowest RAI by fruit bats in this study.

Frugivorous birds have been reported to cause significant economic damage to fruit orchards (Bruggers *et al*., 1998; Maurice *et al*., 2019). However, these previous studies were in line with our findings, where we found high RAI by *P. tricolor* in the litchi orchard, compared to other crop raiders like *C. pygerythrus*, *C. striatus,* and Pteropodidae. These findings were similar to a previous study on weaver birds (*Ploceidae*), reported to cause seasonal crop-yield loss of between 51 and 70% in Tiko, Cameroon (Maurice *et al*., 2019). Similarly, Red-billed quelea (*Quelea quelea*) was reported as the main crop raider of corn (*Zea mays*), rice (*Oryza sativa*), and Pearl millet (*Pennisetum glaucum*) fields in Benue State, Nigeria (Bukie *et al*., 2018). In Kenya, farmers spent most of their daytime (84.8%) guarding their crops against frugivorous bird raids (Musyoki, 2014). In the United State of America (USA), frugivorous birds' damage cost per hectare was estimated at $104 in Oregon tart cherries (*Prunus cerasus*) and $7267 in Washington Honeycrisp apples (*Malus domestica*) orchards (Anderson *et al*., 2013).

Seasonal differences in day length (Caravaggi *et al*., 2018) as well as food abundance (Kunz *et al*., 2011; Taylor *et al*., 2013) have an impact on animal feeding activity resulting in diurnal species foraging more into night hours (Nouvellet *et al*., 2012; Schai-Braun *et al*., 2012). This was similar to our study findings which reported that *P. tricolor* and *C. striatus* increased their foraging activity into nighttime hours during the litchi harvest season (December) in response to litchi crop abundance, compared to litchi pre-harvest season (October/November). However, in South Africa summer days are longer and have more sunshine hours compared to winter season, thus birds can forage more into night hours due to the availability of light. Previous studies also reported that animal activity patterns are influenced by food availability (Pereira, 2010; Prugh and Golden, 2014; Monterroso *et al*., 2014).

Our camera trap study on species richness and activity patterns of fruit bats (*E. wahlbergi, E. crypturus, R. aegyptiacus*), other crop raiders species, and incidentally observed species, provide enough evidence that fruit bats which were thought to be raiders of litchi orchards, and perceived to cause significant economic damage in our study area might be elsewhere. The results from this study revealed that Dark-capped Bulbul is a potential crop raider of litchi fruits in our study area. Therefore, we recommend that research on this species' diet, activity patterns, and foraging ecology must be conducted to gain detailed insight concerning their raids on litchi fruits.

References

ABRAMS, J. F., AXTNER, J., BHAGWAT, T., MOHAMED, A., NGUYEN, A., NIEDBALLA, J. & WILTING, A. (2018). Studying terrestrial mammals in tropical rainforests. a user guide for camera-trapping and environmental DNA. Leibniz-IZW, Berlin.

ADAMS, R. A. & PEDERSEN, S. S. (2013). Bats Evolution, Ecology, and Conservation. New York, *Springler*.

ALBAYRAK, I., ASAN, A. & YORULMAZ, T. (2008). The natural history of the Egyptian fruit bat, *Rousettus aegyptiacus*, in Turkey (Mammalia: Chiroptera). *Turkish Journal of Zoology*, 32,11–18.

ANDERSON, A. M., LINDELL, C. A., MOXCEY, K. M., SIEMER, W. F., LINZ, G. M., CURTIS, P. D., CARROLL, J. E., BURROWS, C. L., BOULANGER, J. R., STEENSMA, K. M. M. & SHWIFF, S. A. (2013). Bird damage to select fruit crops: The cost of damage and the benefits of control in five states. *Crop Protection*, 52, 103-109. http://dx.doi.org/10.1016/j.cropro.2013.05.019.

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. doi:10.3354/esr00441.

ARUMOOGUM, 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.

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*, 377-426. doi 10.1007/978-3-319-25220-9-13

BARNES, R. F. W., BOAFO, Y., NANDJUI, A., DUBIURE, U. F., HEMA, E. E., DANQUAH, E. & MANFORD, M. (2003). An overview of crop raiding by elephants around the Kakum Conservation Area. Part 1 and 2. Elephant Biology and Management Project, Africa Program, Conservation International. Unpublished.

BARRETT, A.S. (2004). Foraging ecology of the vervet monkey (*Chlorocebus aethiops*) in mixed lowveld bushveld and sour lowveld bushveld of the Blydeberg Conservancy, Northern Province, South Africa', MTech dissertation, Department of Environmental Sciences, University of South Africa.

BATES, D., MÄCHLER, M., BOLKER, B. & WALKER, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Software*, 67, 1–48. https://doi.org/10.18637/jss.v067.i01

BEGEMANN, G. J. (2014). The South African Litchi Industry – An overview. *Acta Horticulturae*, 1029, 35-38. https://doi.org/10.17660/ActaHortic.2014.1029.2

BOLKER, B. M., BROOKS, M. E., CLARK, C. J., GEANGE, S. W., POULSEN, J. R., STEVENS, M. H. H. & WHITE, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution*, *24*(3), 127-135.

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. doi:10.3161/150811014X683255.

BUKIE, J. O., YAGER, G. O. & TSAVYANGE, G. A. (2018). Wild animal raid on agricultural crops in Katsina-Ala local government area of Benue State, Nigeria. Proceedings of 6th NSCB Biodiversity Conference; Uniuyo, 49, pp. 52.

BUMRUNGSRI, S., SRIPAORAYA, E., CHONGSIRI, T., SRIDITH, K. & RACEY, P. A. (2009). The pollination ecology of durian (*Durio zibethinus*, *Bombacaceae*) in southern Thailand. *Journal of Tropical Ecology*, 25, 85.

BURTON, A. C., NEILSON, E., MOREIRA, D., LADLE, A., STEENWEG, R, FISHER, J. T, *et al*. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52, 675-685.

CARAVAGGI, A., GATTA, M., VALLELY, M-C., HOGG, K., FREEMAN, M., FADAEI, E., DICK, J. T. A., MONTGOMERY, W. I., REID, N. & TOSH, D. G. (2018). Seasonal and predator-prey effects on circadian activity of free-ranging mammals revealed by camera traps. *PeerJ*, 6: e5827. doi 10.7717/peerj.5827.

CLEVELAND, C. J., FRANK, J. D., FEDERICO, P. & GOMEZ, I. (2006). Economic value of the pest control service provided by Brazilian free-tailed bat in south-central Texas. *Front. Ecol. Environ*, 4, 238–243.

CUTLER, T. L. & SWANN, D. E. (1999). Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin*, 27, 571-581.

CHAO, A., MA, K. H. & HSIEH, T. C. (2016). iNEXT (INterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity. Program and User's Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/.

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 assemblages. *Journal of Plant Ecology*, 5, 3-21.

CRAWLEY, M. J. (2007). The R Book. *Wiley*, 13: 978-0-470-51024-7.

DAFF. (2018). Litchi production guidelines. Republic of South Africa, available online at https//www/dalrrd.gov.za.

DAFF. (2015). Litchi production guidelines. Republic of South Africa, available online at https//www/dalrrd.gov.za.

DE BONDI, N., WHITE, J. G., STEVENS, M. & COOKE, R. (2010). A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. *Wildlife Research*, 37, 456-465.

DVORAKOVA, L., KUCZYNSKI, L., RIVAS-SALVADOR, K & REIF, J. (2022). Habitat characteristics supporting bird species richness in mid-field woodlots. *Front. Environ. Sci*, 10:816255. doi: 103389/fenvs.2022.816255.

FAIRET, E. & MAGU, M. (2012). ‘’Vulnerability to crop-raiding: an interdisciplinary investigation in Loango National Park, Gabon’’. Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/6399.

FINDLAY, L. J. & HILL, R. A. (2020). Baboon and vervet monkey crop-foraging behaviors on a commercial South African farm: preliminary implications for damage mitigation. *Human–Wildlife Interactions*, 14(3), 505–518.

FRONEMAN, I. J. (2010). Horticultural manipulation techniques to improve yield, fruit size and quality in ‘Wai Chee’ litchi (*Litchi chinensis Sonn*.). M. Sc. thesis, University of Kwazulu-Natal, South Africa.

FUJITA, M.S. & TUTTLE, M. D. (1991). Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology*, 5, 455–463.

GOBOSHO, L., FEYSSA, D. H. & GUTEMA, T. M. (2015). Identification of Crop Raiding Species and the Status of Their Impact on Farmer Resources in Gera, Southwestern Ethiopia. *International Journal of Sciences: Basic and Applied Research*, 22 (2), 66-82.

GROVÉ, T., SCHOEMAN, P. S. DE BEER, M. S. (2014). Arthropod pests of litchi in South Africa. *Acta Horticulturae*, 1029, 409–16. https://doi.org/10.17660/ActaHortic.2014.1029.52.

HAJARI, E., NONYANE, D. & CRONJE, R. (2020). Sequence-related amplified polymorphism markers - a tool for litchi breeders in Africa. *South African Journal of Science*, 116, 7-8. http://dx.doi.org/10.17159/sajs.2020/7461.

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.

JENKS, K., CHANTEAP, P., DAMRONGCHAINARONG, K., CUTTER, P., CUTTER, P., REDFORD, T., LYNAM, A., HOWARD, J. & LEIMGRUBER, P. (2011). Using Relative Abundance Indices from Camera-Trapping to Test Wildlife Conservation Hypotheses – An Example from Khao Yai National Park, Thailand. *Tropical Conservation Science*, 4, 113-131. 10.1177/194008291100400203.

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.

KATE, K. (2012). Possible stratergies/practices in reducing wild animal (Primate) crop raids in unprotected areas in Hoima District, conducted in two Sub-Counties in Hoima District, Uganda.

KORINE, C., IZHAKI, I, & ARAD, Z. (1999). Is the Egyptian fruit-bat Rousettus aegyptiacus a pest in Israel? An analysis of the bat's diet and implications for its conservation. *Biol Cons* 88, 301–306.

KUNZ, T. H., DE TORREZ, E. B., BAUER, D., LOBOVA, T. & FLEMING, T. H. (2011). Ecosystem services provided by bats. *New York Academy of Science*, 1223, 1-38. doi:10.1111/j.1749-6632.2011.06004.

LADAN, S. I. (2014). Examining human wildlife conflict in Africa. In: International conference on biological, civil and environmental engineering.

LAN, S. S., ZHANG, Q., HUANG, Q. & CHEN, S. H. (2013). Breeding ecology of Chinese Bulbul in the urban environment of Hangzhou, China. *Zoological Research*, 34(3), 182-189.

LEE, P. C. & PRISTON, N. E. C. (2005). Perception of pests: Human attitudes to primates, conflict and consequences for conservation. In J. D. Paterson & J. Wallis (Eds.), Commensalism and conflict: The human-primate interface (pp. 1–23). Norman, OK: *American Society of Primatologists*.

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//dpi.org/10.1111/j.2041-210X.2010.00063

LINDEN, V. M. G., GRASS, I., JOUBERT, E., TSCHARNTKE, T., WEIER, S. M. & TAYLOR, P. J. (2019). Data from: Ecosystem services and disservices by birds, bats and monkeys change with macadamia landscape heterogeneity. Dryad Digital Repository. *Journal of Applied Ecology*, 56, 2069-2078.

MAURICE, M. E., FUASHI, N. A., MENGWI, N. H., EBONG, E. L., AWA, P. D. & DAIZY, N. F. (2019). The Control Methods used by the Local Farmers to reduce Weaver-Bird Raids in Tiko Farming Area, Southwest Region, Cameroon. *Madridge Journal of Agriculture and Environmental Sciences*. 1 (1), 31-39.

MC GUINNESS, S. & TAYLOR, D. (2014). Farmers` perceptions and actions to decrease crop raiding by forest-dwelling primates around Rhwandan forest fragment. *Human Dimensions of Wildlife*, 19 (2), 179-190. doi: 10.1080/10871209.2014.853330.

MEEK, P. D., BALLARD, G., CLARIDGE, A., KAYS, R., MOSEBY, K., O'BRIEN, T, *et al*. (2014). Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation*, 23, 2321-2343.

MEKONEN, S. (2020). Coexistence between human and wildlife: the nature, causes and mitigations of human wildlife conflict around Bale Mountains National Park, Southeast Ethiopia. *BMC Ecology*, 20.

MEREDITH, M. & RIDOUT, M. (2018). Overview of the overlap package.

MKENDA, P. A., NDAKIDEMI, P. A., MBEGA, E., STEVENSON, P. C., ARNOLD, S. E. J., GURR, G. M. & BELMAIN, S. R. (2019). Multiple ecosystem services from field margin vegetation for ecological sustainability in agriculture: scientific evidence and knowledge gaps. *PeerJ*, 7, e8091. doi: 10.7717/peerj.8091.

MONTERROSO, P., ALVES, P. & FERRERAS, P. (2014). Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: Implications for species coexistence. *Behavioral Ecology and Sociobiology*, 68. 10.1007/s00265-014-1748-1.

MPHETHE, V., WEIER, S., WESTPHAL, C., LINDEN, B, SWANEPOEL, L., PARKER, D. & TAYLOR, P. J. (2023). Epauletted fruit bats prefer native plants and contribute to seed dispersal in a South African agricultural landscape. *African Journal of Ecology*, 00, 1-12. https://doi.org/10.1111/aje.13132.

MUSYOKI, C. (2014). Crop defense and coping strategies: wildlife raids in Mahiga 'B' village in the Nyeri district, Kenya. *African Study Monographs*, 35(1), 19–40.

NOUVELLET, P., RASMUSSEN, G. S. A., MACDONALD, D. W. & COURCHAMP, F. (2012). Noisy clocks and silent sunrises: measurement methods of daily activity pattern. *Journal of Zoology*, *286*(3), 179-184.

O'BRIEN, T. G., KINNAIRD, M. F. & WIBISONO, H. T. (2003). Crouching tigers, hidden prey: sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6(2), 131–139.

OLEKSY, R., RACEY, P. A. & JONES, G. (2015). High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*. *Global Ecology and Conservation*, 3, 678–692.

OLIMPI, E. M., GARCIA, K., GONTHIER, D. J., KREMEN, C., SNYDER, W. E., WILSON-RANKIN, E. E. & KARP, D. S. (2022). Semi-natural habitat surrounding farms promotes multifunctionality in avian ecosystem services. *Journal of Applied Ecology*, 59, 898–908. doi: 10.1111/1365-2664.14124.

PARKER, G. E., OSBORN, F. V., HOARE, R. E. & NISKANEN, L. S. (eds) (2007). Human-Elephant Conflict Mitigation. A training course for Community-based Approaches in Africa. Participant's manual elephant pepper development Trust, Livingstone, Zambia.

PEREIRA, J. A. (2010). Activity pattern of Geoffroy's cats (*Leopardus geoffroyi*) during a period of food shortage. *Journal of Arid Environments*, 74(9), 1106–1109. doi 10.1016/j.jaridenv.2010.03.017.

PRICE, V. (2013). Trouble in paradise: mapping human-wildlife conflict in the western Indian Ocean. Unpublished MSc thesis, Imperial College, London, UK

PRUGH, L. R. & GOLDEN, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*, 83(2), 504–514. doi 10.1111/1365-2656.12148.

R CORE TEAM. (2018). R: A Language and Environment for Statistical Computing.

ROVERO, F., ZIMMERMANN, F. & MEEK, P. D. (2013). Which camera trap type and how many do I need? A review of camera features and study designs for a range of wildlife research. *Hystrix*, 24, 1-9.

SCHAI-BRAUN, S. C., RÖDEL, H. G. & HACKLÄNDER, K. (2012). The influence of daylight regime on diurnal locomotor activity patterns of the European hare (*Lepus europaeus*) during summer. *Mammalian Biology*, *77*, 434-440.

SILESHI, G. W. (2012). A critique of current trends in the statistical analysis of seed germination and viability data. *Seed Sci. Res*, 22, 145–159. https://doi.org/10.1017/S0960258512000025

SMITH, J. A., SURACI, J. P., HUNTER, J. S., GAYNOR, K. M., KELLER, C. B., PALMER, M. S. & BEAUDROT, L. (2020). Data from: Zooming in on mechanistic predator–prey ecology: Integrating camera traps with experimental methods to reveal the drivers of ecological interactions. *Journal of Animal Ecology*, 89, 1997-2012.

SRINIVASULU, C. & SRINIVASULU, B. (2002). Greater short-nosed fruit bat (*Cynopterus sphinx*) foraging and damage in vineyards in India. *Acta Chiropterologica*, 4, 167–171.

STEENWEG, R., HEBBLEWHITE, M., KAYS, R., AHUMADA, J., FISHER, J. T., BURTON, C, *et al*. (2016). Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Frontier in Ecology and the Environment*, 15, 26–34.

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. *Behav. Ecol Sociobiol*, 65, 13-21. doi:10.1007/s00265-010-1037-6.

TAYLOR, P. J., MONADJEM, A. & STEYN, J. N. (2013). Seasonal patterns of habitat use by insectivorous bats in a subtropical African agro-ecosystem dominated by macadamia orchards. *African Journal of Ecology*, 51, 552-561. 10.1111/aje.12066.

THAPA, S. (2021). Roost selection and diet analysis of Leschenaults` Rousette Bat (*Rousettus Leschenaulitii Desmarest*, 1820). M.Sc. Thesis, Tribhuvan University, Nepal. https://elibrary.tucl.edu.np/handle/123456789/9600

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.

VINCENOT, C. E., KOYAMA, L. & RUSSO, D. (2015). Near threatened? First report of unsuspected human driven decline factors in the Ryukyu flying fox (*Pteropus dasymallus*). *Mammalian Biology*, 80, 273–277.

WEBER, N., DUENGKAE, P., FAHR, J, *et al*. (2015). High-resolution GPS tracking of Lyle's flying fox between temples and orchards in central Thailand. *Journal of Wildlife Management*, 79, 957–968.

WELBOURNE, D. J., CLARIDGE, A. W., PAULL, D. J. & LAMBERT, A. (2016). How do passive infrared triggered camera traps operate and why does it matter? Breaking down common misconceptions. *Remote Sensing in Ecology and Conservation*, 2, 77-83.

WELLINGTON, K., BOTTOM, C., MERRILL, C. & LITVAITIS, J. A. (2014). Identifying performance differences among trail cameras used to monitor forest mammals. *Wildlife Society Bulletin*, *38*(3), 634-638.

ZUUR, A. F., IENO, E. N., WALKER, N. J., SAVELIEV, A. A. & SMITH, G. M. (2009). Mixed effects models and extensions in ecology with R. *New York: springer*, 574.

Chapter 4: Perceived and actual ecosystem disservices by fruit bats, birds, and primates in litchi orchards agroecosystems

Vusani Mphethe[1,2], Sina Weier[2,3], Catrin Westphal[4], Birthe Linden[2,5], Lourens Swanepoel[1,2], Daniel Parker[6] and Peter Taylor[2,3].

[1]Department of Biological Sciences, Faculty of Science, Engineering, and Agriculture, Thohoyandou, 0950, South Africa

[2]SARChI Chair on Biodiversity Value and Change, Faculty of Science, Engineering, and Agriculture, Private Bag X5050, Thohoyandou, 0950, South Africa

[3]Department of Zoology & Entomology & Afromontane Research Unit, University of the Free State, QwaQwa Campus, Private Bag X13, Phuthaditjhaba, 9866, South Africa

[4]Functional Agrobiodiversity, Georg-August-University Göttingen, Grisebachstr. 6, 37077 Göttingen, Germany

[5]Lajuma Research Centre, Louis Trichardt, Limpopo Province, South Africa

[6]School of Biology and Environmental Sciences, University of Mpumalanga, Mbombela, 1200, South Africa

Prepared for: Journal of Applied Ecology

Abstract

Ecosystem services and disservices by key animal groups like birds, fruit bats, and primates are often understudied, especially in agroecosystems. This lack of ecological knowledge often results in the persecution and culling of such animals due to perceived damage to fruit trees. In this study, we combined a control-treatment study with questionnaire data to untangle the actual and perceived impact of birds, fruit bats, and primates on litchi (*Litchi chinensis*) orchards, in Limpopo province, South Africa. We tested the hypothesis that caged litchi trees would produce higher yields than controls (not caged) due to reduced damage from vertebrate crop raiders. From questionnaire data, we predicted that both commercial and small-scale litchi farmers would perceive fruit bat damage to be higher than other vertebrates. Finally, we compared actual damage estimates with perceived fruit bat damage on litchi orchards. In contrast to our hypothesis, control trees produced significantly (df = 1, x^2 = 5.021, p = 0.025) higher yields than the caged trees. There was a weak, but non-significant (df = 1, x^2 = 1.015, p = 0.314), trend towards higher vertebrate damage on control trees compared to treatment trees. From farmer questionnaire data, we found that weather (sun/rain) and monkeys were believed to be the main culprits in damaging litchis as compared to fruit bats. There was also strong consensus among farmers that damage varied by vertebrate groups (in order of importance: weather, monkeys, insects, fruit bat, birds, and wild pigs). The type of farm (commercial versus small-scale) also showed a statistically significant difference in perceived damage caused by bats, birds, insects, monkeys, and weather. Our results show relatively low crop raiding incidences by fruit bats. However, reducing persecution will require educating farmers on the ecological importance of these vertebrates and helping enhance ecosystem services.

Keywords: Crop damage, litchis, yield, crop raiding, fruit bats

1. Introduction

Vertebrates such as bats, birds, and primates provide vital ecosystem services to nature (Williams-Guillen *et al*., 2008; Kunz *et al*., 2011; Linden *et al*., 2019). Pteropodids are responsible for the propagation of around 289 plant species of which 186 of which provide economically important products (Labova *et al*, 2009). In the west and east Africa, fruit bats were reported to pollinate Baobabs (*Adansonia digitata*) and Sausage trees (*Kigelia africana*) (Newman *et al*., 2021). Birds have been documented to reduce pest damage in a coffee plantation and prevented an annual yield loss of up to 310 kg per hectare (Karp *et al*., 2013). Together, bats and birds are important biocontrol agents in South African macadamia agroecosystems, with their exclusion amounts to an estimated income loss of USD ~ 5000 per hectare (Linden *et al*, 2019). Furthermore, mammals such as primates are regarded as seed swallowers and spitters (Linden *et al.*, 2015), and can also provide important ecosystem services in the form of seed dispersal (Stinger *et al*., 2020).

Despite the important ecosystem services, beneficial for both natural and agroecosystem environments, these organisms also provide ecosystem disservices, which either reduce productivity or result in increased production costs (Zhang *et al*., 2007). For example, fruit bats have been reported to cause damage to commercial crops around the globe (Aziz *et al*., 2016). In Egypt, Egyptian fruit bat (*Rousettus aegyptiacus*) was regarded to be a highly destructive pest of crops such as mango (*Mangifera indica*), banana (*Musa acuminata*), and peach (*Prunus persica*) (Aziz *et al*., 2016). Similarly, damage caused by Rodrigues flying fox (*Pteropus rodricensis*) and Mauritian flying fox (*P. niger*) on backyard litchi and mango trees was estimated at 36% and 42% in Mauritius (Price, 2013; Tollington *et al*., 2019). These losses resulted in the government of Mauritius ordering a major cull of these animals (between 2015/2016 and 2018/2019), hence their move from Vulnerable to Endangered in the IUCN Red List of Threatened Species (Kingston *et al*., 2018; IUCN, 2018; Tollington *et al*., 2019). Similarly, the human-animal conflict between fruit farmers and *R. aegyptiacus* led to the extermination of this species in Israel (Korine *et al*., 1999). Fruit bats are also believed to damage litchi fruits in South Africa`s agroecosystems (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986). However, primates such as monkeys are known for their crop-raiding activity due to their opportunistic foraging behavior (Lee & Priston, 2005). Similarly, Olive baboon (*Papioanubis*) raids on maize, teff, and sorghum fields were reported in Ethiopia (Gobosho *et al*., 2015). Monkeys and baboons cause annual crop damage of USD 5,251,648 to South African Macadamia Growers (Linden *et al*., 2019).

The South African litchi farming industry has reported that fruit bats raid litchi orchards, especially during litchi harvest season, when the crop is ripe (Jacobsen & du Plessis, 1976; Jacobsen *et al*., 1986). However, litchi trees host a variety of pests, including birds (Dark-capped Bulbuls [*Pycnonotus tricolor*]; Speckled Mouse birds [*Colius striatus*]), insects (fruit flies [*Ceratitis* spp.]; litchi moth [*Cryptophlebia peltastica*]; false codling moth [*Thaumatotibia leucotreta*]) and primates (vervet monkey [*Cercopithecus pygerythrus*)]). Quantifying the role of these pests, both empirical via control treatment designs, and informal via questionnaires remains unexplored. In this study, we aimed to quantify the damage caused by fruit bats, birds, and primates, using exclusion experiments on two litchi farms over two consecutive harvesting years. We further aimed to compare the actual litchi crop damage to perceived damage by conducting questionnaire surveys.

We hypothesized that the absence of crop-raiding vertebrates such as bats, birds, and monkeys would decrease damage to litchi fruits. We further predicted that farmers might perceive damage by fruit bats to be higher than other vertebrates. We finally hypothesized that the absence of crop raiding vertebrates such as fruit bats and monkeys would decrease damage to litchi fruits, but by removing insectivorous birds and bats would increase the damage. We therefore predicted that, while removal of large crop raiders may increase yield for caged litchi trees, removal of insectivorous bats and birds may decrease yield due to insect damage.

2. Materials and methods

2.1 Study area and exclusion experiments design

2.1.1 Neuhoff Farm

The study area was situated in Neuhoff Farm (-23.06588879S, 30.0783689E), located on the foothills of the Soutpansberg Mountain Range (855 m above sea level), about 20 km east of Louis Trichardt town (Figure 12). The size of the study area is about 183 ha and characterized by litchi, macadamia (*Macadamia integrifolia*), avocado (*Persea americana*) and pecan (*Carya illinoinensis*) orchards. Regarding cropping, the area is dominated by macadamia (47.10 ha; 25.74%), followed by avocado (16.69 ha; 9.12%), litchi (2.47 ha; 1.35%), and pecan (1.20 ha; 0.66%). 29.5% of the study farm is comprised of the natural vegetation of dense thickets classified as Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006). Neuhoff Farm produces an annual total yield of 83 tons of litchis during the harvest season in December/January. The area receives an annual summer rainfall of between 930 mm and 960 mm and fell mostly between November and April (Taylor *et al*., 2013b).

2.1.2 Rionde Fruit Farm

Rionde Fruit Farm/Gilbert Packer (-23.0722691S, 30.08265997E) was our second study area neighboring Neuhoff Farm (Figure 12) and located on the foothills of the Soutpansberg Mountain Range (888 m above sea level). The size of this study area is about 240 ha and characterized by litchi, macadamia, and avocado orchards. In terms of cropping the area is dominated by macadamia (90 ha; 37.50%), followed by avocado (50 ha; 20.83%) and litchi (33 ha; 13.75%). Rionde Fruit Farm produces an annual litchi yield of 250 tons during the harvest season in December/January. The study site also receives an annual rainfall pattern similar to Neuhoff Farm.

The two study sites (Figure 12) in Levubu (where our exclusion experiments were conducted) cultivated the Mauritius cultivar which dominates all the production areas in South Africa. The other study sites where questionnaire surveys were conducted cultivated litchi varieties including Mauritius, Chinese, and Madras cultivars. Litchi (*Litchi chinensis*) belongs to the family Sapindaceae (Greer, 1996, Froneman, 2010), and originated from the region between southern China and northern Vietnam (Stern and Gazit, 2003). The first litchi plants were imported from the Island of Mauritius around 1876 (Oosthuizen, 1993), with some trees already being noticed in KwaZulu Natal in the year 1876 which indicates earlier import (DAFF, 2013).

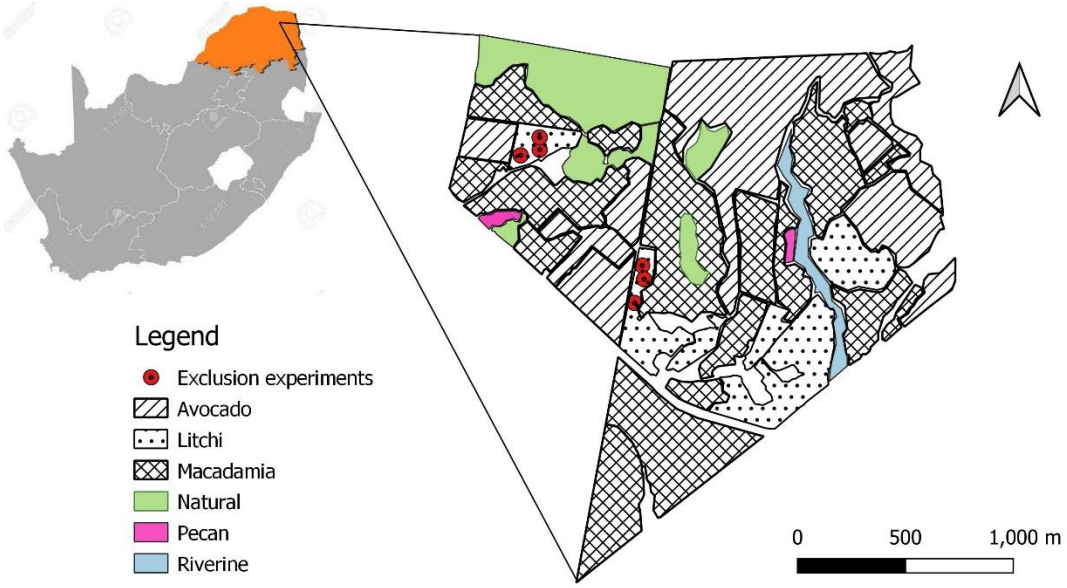


Figure 12 Map showing the study area and major habitat types of the two farms situated in the Levubu subtropical crop growing area (Red circles = Full Exclosure and Open Control experiments), South Africa.

2.2 Experimental design

The experimental exclusion took place over two consecutive litchi harvest seasons, during 2019 and 2020. A total of 6 cages were constructed, each enclosing one litchi tree with a nylon mesh net with a 2×3cm mesh size that only allows arthropods or small animals (e.g., ants, moths, spiders) to enter but excludes flying vertebrates (bats and bird), monkeys and large herbivores (Figure 13). The exclusion cages were constructed in August 2019 (we selected trees which were healthy and have more flowers), three months before litchi fruit harvest, and the cages were left in the orchards until following fruiting period/season. The exclusion cages were taken down after the 2020 litchi harvest period when sampling was concluded. We applied two treatments on our two study sites, the "FULL" exclosure which was closed all times (to prevent bats, birds, and monkeys to access the tree), and the "CONTROL" (open at all times and without frames or nets). Each treatment was paired with an adjacent plot (CONTROL) of the same area as the cage (FULL) marked with a taper (danger tape) and resulted in three paired treatments on each farm.

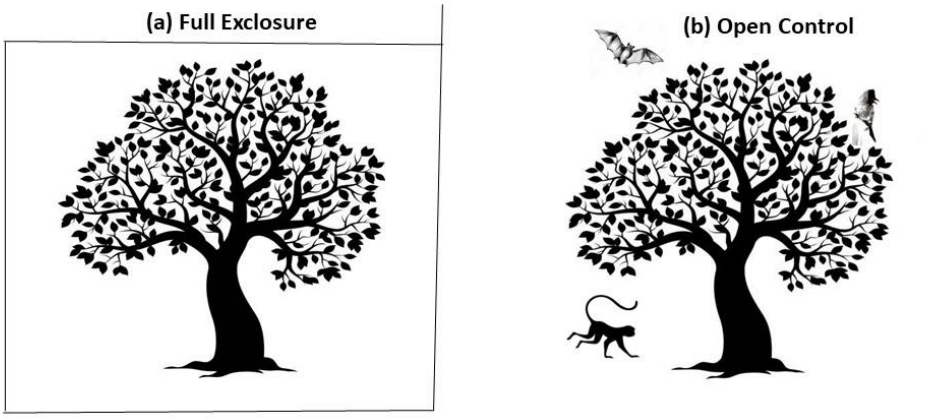


Figure 13 Exclusion experiment setup between the two litchi farms in Levubu; (a) Full Exclosure preventing bats, birds, monkeys, and big herbivores from entering the cage and (b) Open Control which allows vertebrates to access the tree/fruits.

2.3 Yield

Litchi harvesting is done during December/January each year when the fruits are mature and have an average mass of between 21 and 25 g (DAFF, 2013). The total yield for each tree (FULL and CONTROL) was determined by measuring the total mass of the fruits produced by each tree from our two study sites (Figure 14). We used Linear Mixed Effect Models (LMM) to investigate the effects of vertebrate's exclusions on litchi crop yield. LMMs are preferred models for the analysis of yield data (Brown, 2020). We modelled treatments (FULL exclosure and open CONTROLS) as fixed effects to evaluate the effects of net enclosures on litchi crop yield (total yield). We also included plots and farms (Neuhoff Farm and Rionde Fruit Farm) as random effects to account for natural variation in yield between individual trees. The actual litchi fruit damage (rejects) was also modelled in the same manner as the total yield for both treatments (FULL exclosure and open CONTROL). The actual litchi fruit damage between the two farms (Neuhoff Farm and Rionde Fruit Farm) was also modelled using LMM with farm names as fixed effects. The models were fitted in R version 3.5.1. (R Development Core Team 2008) using the lmer package.

Figure 14 Litchi crop yield assessment between (a) Open Controls and (b) Full Exclosure experiments during harvest season in Levubu.

2.4 Questionnaire surveys

A questionnaire survey was used to assess the opinions of litchi farmers concerning the damage caused by fruit bats, birds, insects, monkeys, and weather (sun/rain) to their produce (Appendix F). We designed two kinds of questionnaire surveys, the online Google survey aimed at commercial litchi farmers and the face-to-face survey aimed especially at small-scale litchi farmers. The overall questionnaire surveys were completed by a total of 51 respondents, of which 13 respondents were commercial farmers, and 38 were small-scale farmers. Interviewees' details, farm characteristics, litchi crop income, and other potential income sources and their revenues were asked. The interviewees were also asked about fruit bats raids, which variety is more susceptible to fruit bats damage, the relative number of litchi skin found in the orchards during fruiting season, their annual litchi yield, and how much is damaged by fruit bats, insects, birds, weather (sun/rain), monkeys and other sources of damage. We further asked the interviewees whether they meet experts concerning fruit bats control, control measures they use to prevent litchi damage and whether the control method is effective or not, what animal they target for pest control and their estimated annual cost, how they feel towards bats and other animals, their knowledge on fruit bat ecosystem services to the

environment, and lastly what method do they think would be most successful to control fruit bats. The ethical approval for this study was provided by the University of Venda Ethics Committee (Research Ethics Clearance Project Number: SMNS/19/ZOO/04/1909). We also obtained informed consent from each person we interviewed and informed them that their anonymity would be maintained.

To determine whether there was a statistical difference between the damage caused by bats, birds, insects, monkeys, weather, and wild pigs, as well as over different locations where the questionnaire survey was conducted, and between damage between commercial and small-scale litchi farmers, a non-parametric Kruskal-Wallis test was used. All statistics were done in R (R Development Core Team, Vienna, available at http://www.r-project.org, accessed 2022).

3. Results

3.1 Yield

Litchi total yields were significantly lower in the Full exclosures (M = 57.13, SD = 38.93) than in the Open controls (M = 99.7, SD = 61.09) (df = 1, x^2 = 5.021, p = 0.025; Figure 15).

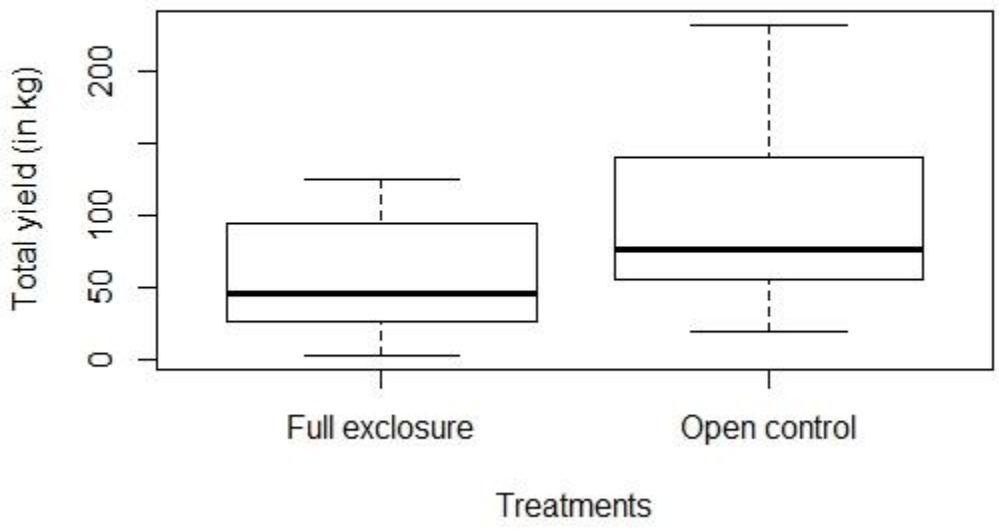


Figure 15 Total litchi crop yield at the two litchi farms in Levubu between Full exclosure and Open control experiments for the 2019/2020 litchi harvest season. The boxes show median (solid black line

across the box), and 1st (top box) and 3rd (bottom box) quartiles. Whiskers show the total range and dots outside of the boxes indicate outliers.

There was no significant difference in litchi damage (rejects) in the Open controls (M = 6.7, SD = 4.22) compared to the full exclosures (M = 4.99, SD = 4.53) (df = 1, x^2 = 1.015, p = 0.314). Similarly, we found no significant difference in litchi damage (rejects) between the two sites (Neuhoff Farm [M = 7, SD = 5.32] and Rionde Fruit Farm [M = 4.7, SD = 2.95]; df = 1, x^2 = 1.53, p = 0.216).

3.2 Questionnaire surveys

Over sixty percent (61%) of the commercial farming respondents reported that they have observed fruit bats raiding their litchi orchards every night, and 15% of those said they have seen bats twice a week (Figure 16a). However, 8% of the respondents reported having not seen fruit bats raiding their orchards, once in two nights, or that they were difficult to track, respectively (Figure 16a). However, about forty percent (38%) of the commercial farming respondents reported that they have commonly observed litchi skin/spit outs on the ground in litchi orchards during the fruiting season, with a further 31% of the respondents reporting that they have never seen litchi skin in their orchards (Figure 16b). Approximately 31% of the respondents reported to having seen plentiful litchi skin/spit outs on the ground during litchi fruiting season.

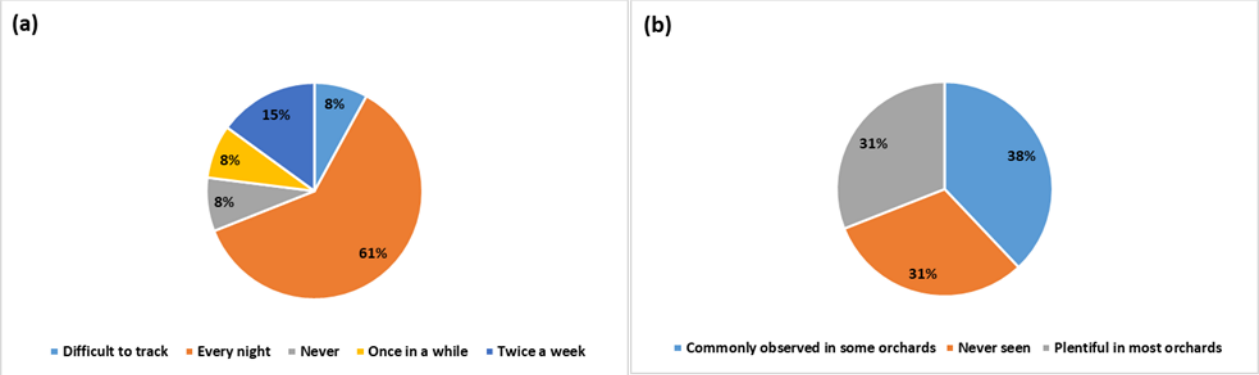


Figure 16 Percentage of respondents (n = 13, commercial farmers) on (a) how often fruit bats raid their orchards during the fruiting season; (b) litchi skin/spit outs found on the ground during litchi fruiting season.

Small-scale farming respondents reported similar patterns to the commercial farming respondents with over fifty percent (52%) reporting to have observed fruit bats raiding their litchi orchards every night, and 24% of those saying that they have seen bats twice a week. However, 16% of the respondents reported having not seen fruit bats raiding their orchards, and 8% reported having seen fruit bats once in two nights (Figure 17a). Sixty-four percent (64%) of the small-scale farming respondents reported that they commonly observed litchi skin/spit outs on the ground in litchi orchards during fruiting season, with 18% of the respondents reporting that they had never seen litchi skin in their orchards (Figure 17b). Eighteen percent of the respondents reported having seen plentiful litchi skin/spit outs on the ground during litchi fruiting season.

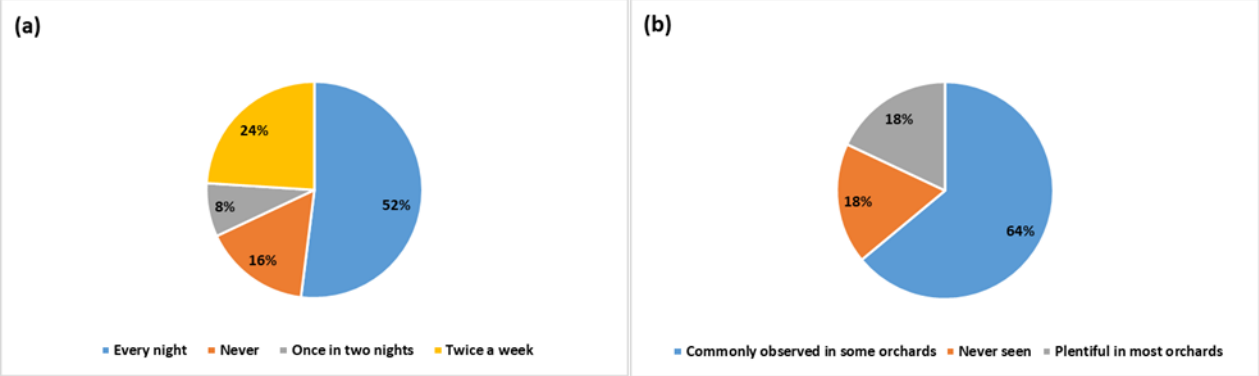


Figure 17 Percentage of respondents (n = 38, small-scale farmers) on (a) how often fruit bats raid their orchards during the fruiting season; (b) litchi skin/spit outs found on the ground during litchi fruiting season.

There was a statistically significant difference in the reported damage-causing agents as reported by farmers (df = 5, x^2 = 88.11, p < 0.001). Weather (28%) was reported to inflict the highest damage on commercial farms (Figure 18a), followed by monkeys, insects, and fruit bats (27%, 21%, and 19%), respectively. However, the damage caused by birds (5%) was lower compared to weather (sun/rain), monkeys, and insect damage. Similarly, small-scale farming respondents reported monkeys (32%) and weather (29%) as the main cause of damage followed by fruit bats (17%), and insect (16%) in litchi orchards (Figure 18b). Farm type (commercial versus small-scale) show a statistical significant difference (df = 1, x^2 = 37.12, p < 0.001) in the perceived damage caused by bats, birds, insects, monkeys, weather and wild pigs. However, commercial farmers reported higher damage compared to small-scale farmers.

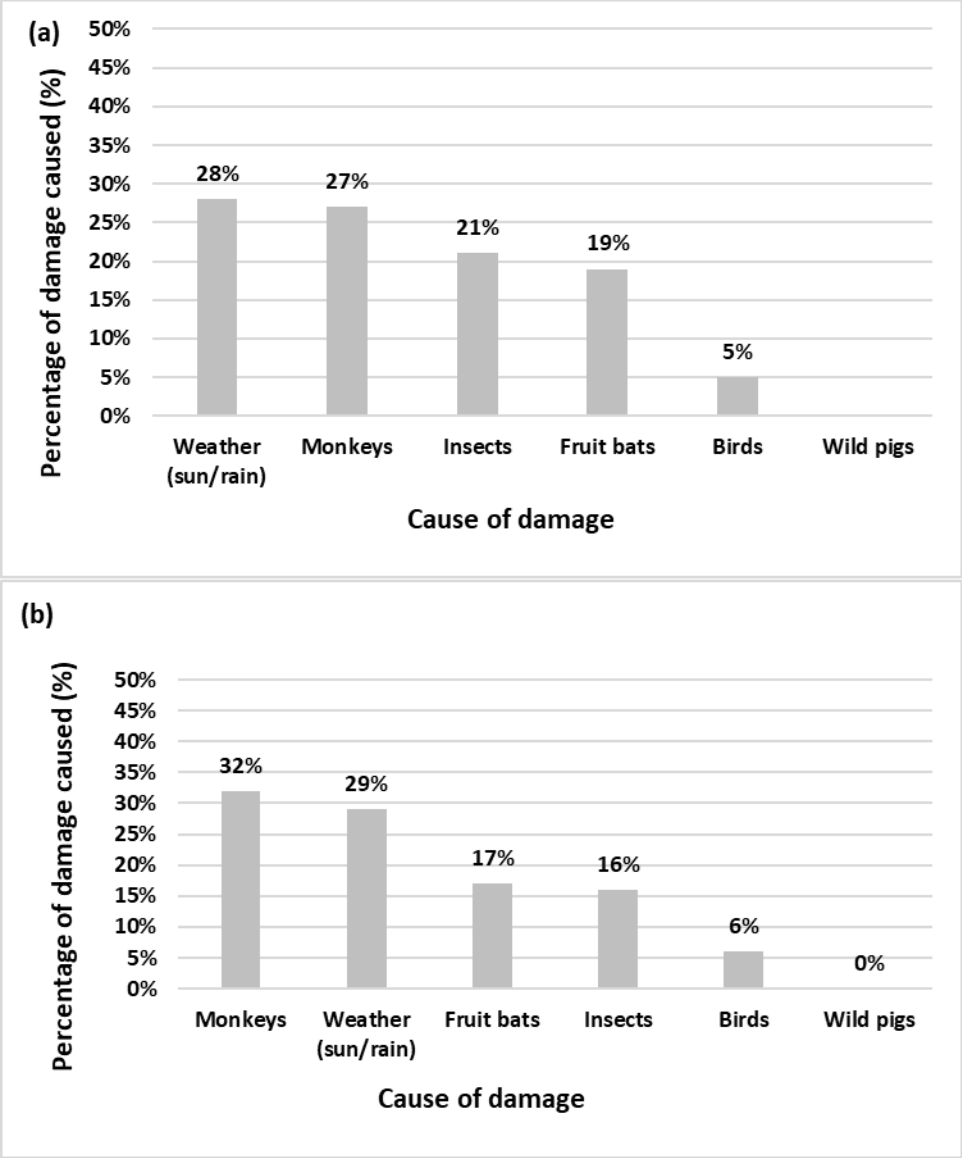


Figure 18 Percentage of the perceived damage caused by weather, monkeys, insects, fruit bats, birds, and wild pigs during the fruiting season on (a) commercial, and (b) small-scale farms.

Over seventy percent (76%) of the commercial farming respondents reported feeling good about fruit bats and other animals, and 8% felt neutral, angry, or had nothing to say, respectively (Table 4). However, a high number of respondents (69%) did not know about the ecosystem services provided by fruit bats to the environment, whilst only 31% reported knowing about the benefits of having fruit bats in the environment. Concerning the control measures for fruit bat damage, a higher percentage of commercial farming respondents (46%) suggested the use of deterrents as a solution for crop raiding, 23% suggested netting, and 8% reported the use of decoy crops. By contrast, small-scale

farming respondents (74%) reported that they have negative feelings towards fruit bats (feel bad) and other animals, with only 24% reporting that they have positive feelings (feel good). Like the commercial farming respondents, a higher percentage of small-scale farming respondents (66%) knew nothing about fruit bats' ecosystem services to the environment, with only 32% of the respondents having some knowledge of fruit bats' ecosystem services (Table 4). Small-scale farming respondents (40%) suggested netting as a solution for crop raiding, with 26% suggesting shooting/ killing as a suitable control measure. However, 21% suggested the use of deterrents, and 8% the use of biological agents, with 5% of the respondents suggesting fruit bagging as a control measure.

Table 4 Percentage of respondents (n = 13 for commercial farmers and n = 38 for small-scale farmers) with responses to questions on fruit bats and other animal perception, fruit bat ecosystem services knowledge, and fruit bat control measures.

	How do you feel toward bats and other animals?			Do you feel you know much about the ecosystem services fruit bats provide to the environment?			What would be the most successful method to control the bat?	
	Commercial	Small-scale		Commercial	Small-scale		Commercial	Small-scale
Positive feeling (Good)	76	24	Yes	31	32	Biological agents	0	8
Negative feeling (Bad)	0	74	No	69	66	Decoy crops	8	0
Nothing to say	8	2	Nothing to say	0	2	Deterrents	46	21
Anger	8	0				Fruit bagging	0	5
Neutral	8	0				Netting	23	40
						Nothing to say	23	0
						Shooting	0	26

4. Discussion

Contrary to our hypothesis and other studies (Tollington *et al*., 2019), we found that the exclusion of fruit bats, birds, and monkeys led to a decrease in litchi yield during harvest season as compared to controls. We provide several, not mutually exclusive, reasons for these results. First, the exclusion of insectivorous bats and birds could have provided an advantage to pest insects such as litchi moths (*C. peltastica*) and false codling moths (*T. leucotreta*) which could outweigh any direct costs of fruit bats and birds in terms of litchi damage and yield. These arthropods are reported to cause significant damage to litchi crops in South Africa (Schoeman and Mohlala, 2012; Grove *et al*., 2014). Insectivorous bats and birds have been documented to significantly reduce arthropod abundance in agroecosystems (Williams-Guillen *et al*., 2008; Mass *et al*., 2013; Linden *et al*., 2019). Bats respond to pest insect abundance (Arlettaz *et al*., 2001; MacCracken *et al*., 2012; Taylor *et al*., 2013b), and recent studies recorded DNA of agricultural pest species in the diet of insectivorous bats foraging in an agroecosystem (Cleveland *et al*., 2006; Bohmann *et al*., 2011; Kunz *et al*., 2011, Taylor *et al*., 2013*a*). Secondly, netting may have created an unfavorable microclimate for the litchi trees resulting in poor fruit yield and lower fruit quality. Litchi trees requires sunlight duration of over 1700 hours per annum (Xie *et al*., 2023). Sunlight facilitates the process of photosynthesis, increase the accumulation of photosynthetic substances in litchi fruit, as well as fruit quality (Liu *et al*., 2022). Nets have been reported to alter orchards' microclimate and light deprivation resulting in decreased fruit quality (Solomakhin & Blanke, 2007). The Primsole mandarin fruits (*Miho satsuma* × *Carvalhais mandarin*) covered with dark-coloured nets show lower fruit yield when compared to other treatments (white, grey, temporarily shaded, and open controls) in eastern Sicily (Germana *et al*., 2003). Nets applied over 'Hamlin' orange orchards reported reduced yield and fruit weight (Syvertsen *et al*., 2003). Furthermore, the application of nets on mandarin trees resulted in reduced fruit weight and size (Mataa & Tominaga, 1998). Moreover, we recommend that future studies should also look at the effect of netting on tree photosynthesis, crop yield, and fruit quality. Lastly, netting may have granted less access for pollinators, and only allow fewer fruits/flowers to be pollinated. Bees (*Apis*) are important pollinators of litchi flowers in South African agroecosystems (Melin *et al*., 2014). However, exclusion nets may provide a physical barrier that discourage pollinators such as bees from accessing the flowers (Walsh *et al*., 2006). Furthermore, the absence of pollinators could result in reduced fruit set and low fruit yield (Zilkah *et al*., 2013; Garcia-sanchez *et al*., 2015). Previous studies reported that 75% of crop species utilized as food sources rely on insect pollination to produce a good yield (Klein *et*

al., 2007; Garibaldi *et al*., 2013). Insect exclusion resulted in a decrease in yields from crops covered with nets in Europe`s agroecosystems (Bartomeus *et al*., 2014). However, the pollination of coffee (*Coffea canephora*) plants by bees have resulted in increased fruit set and coffee yield in Indonesia (Klein *et al*., 2003). Furthermore, pollinator exclusion from female pumpkin flowers (*Cucurbita moschata*) resulted in the plants aborting their fruits (Hoehn *et al*., 2008).

Even though we empirically failed to find an impact on yield due to exclusion, several studies have reported success in reducing crop damage by using nets. For example, in Mauritius, fruit yield from litchi pinnacle covered with nylon nets was one-third greater when compared to uncovered pinnacle (Tollington *et al*., 2019). In Australia. netting successfully protected fruits from flying foxes and hail damage, and hence facilitate early fruit ripening (Adams & Pedersen, 2013). Aziz *et al*., (2016) reported that netting reduces significant fruit damage from animal pests such as fruit bats, birds, and other mammals in an agroecosystem (Aziz *et al*., 2016). Exclusion nets significantly reduced the damage caused by fruit moths (*Halyomorpha halys* and *Drosophila suzukki*) by 90% and 78%, respectively, and allows for the production of healthier nectarine fruits due to reduced application of insecticides (Candian *et al*., 2021). Tinyane *et al*., (2018) reported an improved yield and accelerated ripening for Hass avocado fruit harvested from under exclusion netting.

Failure to control crop raiding by vertebrates often leads to persecution. For example, Pteropodids such as flying foxes were regarded as pests in agriculture and legally culled to reduce the damage they caused to commercial fruits (Bumrungsri *et al*., 2009). The Mauritius fruit bat (*P. niger*) was legally culled due to public and fruit-growing farmers on perceived damage to their fruits including litchis (Tollington *et al*., 2019). Dawn bat (*Eonycteris spelaea*) pollination of durian trees (*Durio zibethinus*) in Thailand has resulted in the killing of this species due to a misconception that they were feeding destructively on the flowers (Aziz *et al*., 2016). Moreover, in South Africa fruit-eating bat species such as the Egyptian fruit bat was persecuted due to the damage they cause to litchi fruits (Jacobsen & du Plessis, 1976; Jacobsen *et al*., 1986).

The findings from our study on litchi crop yield have shown lower reject fruits inside exclusion cages, compared to paired controls. These findings were similar to previous studies which documented that full exclusion netting is the most effective way to control the damage caused by fruit bats and birds (Tillman *et al*., 2000; Government Queensland, 2009; Aziz *et al*., 2016). In Mauritius, it was documented that enclosing litchi tree pinnacles within net bags significantly reduced the amount of fruit loss to birds and bats (Tollington *et al*., 2019).

Single-row exclusion nets were documented to effectively control bird damage without causing a significant impact on the animal in southeastern France (Bouvier *et al*., 2022). The use of exclusion nets on litchi and mango trees resulted in reduced damage by the Mauritian flying fox (*P. niger*) in Mauritius (Oleksy *et al*., 2018).

Fruit bats are disliked and often persecuted by farmers due to the economic damage they cause to ripe fruits (Jacobsen *et al*., 1986; Fleming *et al*., 2009; Aziz *et al*., 2016; Tollington *et al*., 2019). In our study, we found that the majority of the respondents (commercial and small-scale) reported having observed fruit bats raiding their orchards every night and commonly finding litchi skin/spit outs on the ground during the litchi fruiting season. Moreover, weather and monkeys were perceived by both commercial and small-scale farmers to cause more damage to litchis than fruit bats. Furthermore, our study also revealed that most commercial farmer's respondents perceived fruit bats as "good creatures". This was opposite to the small-scale farmers, with the majority perceiving fruit bats as "bad creatures", and this contrast may be due to a lack of knowledge of the vital ecosystem services provided by bats. Huang *et al*. (2014), Adams and Pedersen (2013), and Aziz *et al*. (2016) all documented an urgent need to educate fruit growers on the ecological and economic importance of fruit bats, thereby mitigating lethal conflict. Significantly, in the Mascarene Islands, public education programs led to an increase in Rodrigues fruit bat (*P. rodricensis*) population (Adam & Pedersen, 2016). Studies on bat diet have also documented that fruit bats prefer to feed on native fruits compared to commercial fruits (Korine *et al*., 1999; Del Vaglio *et al*., 2011; Andrianaivoarivelo *et al*., 2012), with other studies reporting that depletion of food sources because of habitat loss led to commercial fruit raiding (Nakamoto *et al*., 2007; Luskin, 2010). Such studies encourage the maintenance of wild sources through the conservation and planting of wild food sources as a further measure to reduce conflict between farmers and fruit bats.

Interestingly, the results from our questionnaire survey revealed that the majority of small-scale farmer`s respondents believed that the use of nets to exclude fruit bat depredation on litchi fruits might be effective. This finding agrees with previous research which has documented the use of exclusion netting as an effective method to prevent fruit loss to bats and birds (Minifie & Willis, 1990; Hall & Willis, 1992; Campbell & Greer, 1994). Exclusion nets are expensive, especially for small-scale farmers, and require substantial investment when damaged (Ullio, 2002; Don't Shoot Bats, 2013). The annual cost of leasing or buying exclusion netting can therefore exceed the cost of the damage caused by fruit bats (Comensoli, 2002). However, the small-scale farmer respondents in our study also suggested

shooting/killing as a control measure to prevent fruit bat damage to litchi fruits. Such an attitude goes against previous studies which have suggested that shooting is not an effective method to prevent fruit bat damage (Thiriet, 2010). Most fruit bat damage is reported when their native food sources are in short supply either due to droughts or nectar washout (Aziz *et al*., 2016). The majority of commercial farmers felt that the use of deterrents may be effective in controlling fruit bat damage to their litchi orchards. This belief agrees with a previous study that documented that casting distress or alarm calls is one of the promising noise deterrent methods to control fruit bats' damage in fruit orchards (Aziz *et al*., 2016).

Our litchi yield results over two consecutive seasons, coupled with a questionnaire survey study provided enough evidence that fruit bats in our study area do not raid litchi orchards. However, the results from our questionnaire survey on perceived damage have shown that bat ecosystem services are not very well understood and public education is needed in the farming community. Questionnaire surveys would have worked better if a large farming community of commercial litchi farmers similar to the one in Tzaneen and Mpumalanga had been interviewed face to face instead of through using google survey forms. A previous study (Tollington *et al*., 2019) on quantifying fruit bat damage on litchi crops produced good results, as a result, future studies should consider an assessment of signs of damage on the fruits from insects, bats, birds, and weather.

References

ADAMS, R. A. & PEDERSEN, S. S. (2013). Bats Evolution, Ecology, and Conservation. New York, *Springler*.

ARLETTAZ, R., CHRISTE, P., LUGON, A *et al*. (2001). Food availability dictates the timing of parturition in insectivorous mouse-eared bats. *Oikos* 95,105–111

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. doi: 10.3354/esr00441

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*, 377-426. doi 10.1007/978-3-319-25220-9_13

BARTOMEUS, I., POTTS, S. G., STEFFAN-DEWENTER, I., VAISSIERE, B. E., WOYCIECHOWSKI, M., KREWENKA, K. M., TSCHEULIN, T., ROBERTS, S. P. M., SZENTGYORGYI, H., WESTPHAL, C. & BOMMARCO, R. (2014). Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ*, 2, e328; doi 10.7717/peerj.328

BOHMANN, K., MONADJEM, A., NOER, C. L., RASMUSSEN, M., ZEALE, M. R. K., CLARE, E., JONES, G., WILLERSLEV, E. & GILBERT, M. T. P. (2011). Molecular diet analysis of two African free–tailed bats (Molossidae) using high throughput sequencing. *PLoS One*, 6, e21441. doi:10.1371/journal.pone.0021441.

BOUVIER, C. J., BOIVIN, T. & LAVIGNE, C. (2022). Single-row exclusion nets: an alternative pest control method with no detectable impact on breeding bird assemblages in orchards bordered by hedgerows. *Agronomy for Sustainable Development*, 42, 23. https://doi.org/10.1007/s13593-021-00743-7

BROWN, V. A. (2020). An introduction to linear mixed-effects modelling in R. *Association for Psychological Science*. 4, 1–19. https://orcid.org/0000-0001-5310-6499

BUMRUNGSRI, S., SRIPAORAYA, E., CHONGSIRI, T., SRIDITH, K. & RACEY, P. A. (2009). The pollination ecology of durian (Durio zibethinus, Bombacaceae) in southern Thailand. *Journal of Tropical Ecology*, 25, 85.

CAMPBELL, J. & GREER, N. (1994). Controlling pest losses—why, how, how much? In: Bird and bat control for horticulture and aquaculture, Nambour, Queensland, 18 May 1994. Seminar proceedings, Department of Environment and Heritage, Queensland, pp 38–41

CANDIAN, V., PANSA, M. G., SANTORO, K., SPADARO, D., BRIANO, R., PEANO, C. *et al*. (2021). First multi-target application of exclusion net in nectarine orchards: effectiveness against pests and impact on beneficial arthropods, postharvest rots and fruit quality. *Insects*, 12, 210.

CLEVELAND, C. J., BETKE, M., FEDERICO, P., FRANK, J. D., HALLAM, T. G., HORN, J., LOPEZ ´, J. D. JR., MCCRACKEN, G. F., MEDELLÍN, R. A., MORENO-VALDEZ, A., SANSONE, C. G., WESTBROOK, J. K. & KUNZ, T. H. (2006). Economic value of the pest control service provided by Brazilian free–tailed bats in south–central Texas. *Frontiers in Ecology and the Environment*, 4, 238–243.

COMENSOLI, P. (2002). The impact upon fruit growers of a decision to list the grey-headed flying fox as a Vulnerable species under the NSW Threatened Species Conservation Act. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. *Royal Zoological Society of New South Wales*, Mosman, NSW, pp 53–55

DAFF, (2013). Litchi production guidelines. Republic of South Africa.

DEL VAGLIO, M. A., NICOLAU, H., BOSSO, L et al. (2011). Feeding habits of the Egyptian fruit bat Rousettus aegyptiacus on Cyprus island: a first assessment. *Hystrix Ital J Mamm*, 22, 281–289

DON'T SHOOT BATS. (2013). Lethal crop protection is not effective. http://www.dontshootbats.com/ crop-protection.html. Accessed 11 October 2022

FLEMING, T. H., GEISELMAN, C. & KRESS, W. J. (2009). The evolution of bat pollination – a phylogenetic perspective. *Annals of Botany*, 104, 1017-1043. doi:10.1093/aob/mcp197, available online at www.aob.oxfordjournals.org

FRONEMAN, I. J. (2010). Horticultural manipulation techniques to improve yield, fruit size and quality in 'Wai Chee' litchi (Litchi chinensis Sonn.). Unpublished MSc thesis, University of KwaZulu Natal, South Africa.

GARCÍA-SÁNCHEZ, F., SIMÓN, I., LIDÓN, V., MANERA, F. J., SIMÓN-GRAO, S., PÉREZ-PÉREZ, J. G. & GIMENO, V. (2015). Shade screen increases the vegetative growth but not the production in 'Fino 49'lemon trees grafted on Citrus Macrophylla and Citrus aurantium L. *Scientia Horticulturae*, 194, 175–180.

GARIBALDI, L. A., STEFFAN-DEWENTER, I., WINFREE, R., AIZEN, M. A., BOMMARCO, R., CUNNINGHAM, S. A., KREMEN, C., CARVALHEIRO, L. G., HARDER, L. D., AFIK, O., BARTOMEUS, I., BENJAMIN, F., BOREUX, V., CARIVEAU, D., CHACOFF, N. P., DUDENHOFFER, J. H., FREITAS, B. M., GHAZOUL, J., GREENLEAF, S., HIPOLITO, J., HOLZSCHUH, A., HOWLETT, B., ISAACS, R., JAVOREK, S. K., KENNEDY, C. M., KREWENKA, K. M., KRISHNAN, S., MANDELIK, Y., MAYFIELD, M. M., MOTZKE, I., MUNYULI, T., NAULT, B. A., OTIENO, M., PETERSEN, J., PISANTY, G., POTTS, S. G., RADER, R., RICKETTS, T. H., RUNDLOF, M., SEYMOUR, C. L., SCHUEPP, C., SZENTGYORGYI, H., TAKI, H., TSCHARNTKE, T., VERGARA, C. H., VIANA, B. F., WANGER, T. C., WESTPHAL, C., WILLIAMS, N. & KLEIN, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, 339(6127), 1608–1611. DOI 10.1126/science.1230200.

GERMANA, C., CONTINELLA, A. & TRIBULATO, E. (2003). Net shading influence on floral induction on citrus trees. *Acta Horticulturae*, 614, 527–533.

GOBOSHO, L., FEYSSA, D. H. & GUTEMA, T. M. (2015). Identification of Crop Raiding Species and the Status of Their Impact on Farmer Resources in Gera, Southwestern Ethiopia. *International Journal of Sciences: Basic and Applied Research (IJSBAR)*, 2, 66-82.

GOVERNMENT QUEENSLAND. (2009). Flying fox control methods research. Department of Agriculture and Fisheries. Government of Australia. https://www.daf.qld.gov.au/business-priorities/plants/weeds-pest animals-ants/pest-animals/control-methods/flying-fox-control-methods-research

GREER, N. G. (1996). The international lychee scene. Proceedings of the Fourth National Lychee Seminar Including Longans: 'From Marcott to Market' (Welch, T & Ferguson, J., eds), pp. 1-10.

GROVE, T., SCHOEMAN, S. & BEER, M. S. (2014) Arthropod pests of litchi in South Africa, *Acta Horticulturae*, 1029, 409-416.

HALL, J. & WILLIS, B. (1992). Netting orchards against flying foxes, birds, and hail. In: BLADE, K (ed) Fruit crop protection seminar. NSW National Parks and Wildlife Service, Australia, pp 24–28.

HOEHN, P., TSCHARNTKE, T., TYLIANAKIS, J. M. & STEFFAN-DEWENTER, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. B*, 275, 2283–2291. doi:10.1098/rspb.2008.0405

HUANG, J. C-C., JAZDZYK, E., NUSALAWO, M, *et al*. (2014). Is Bat coffee a potential "wing-wing" tool for biodiversity conservation in southwestern Sumatra? Paper presented at the 16th international bat research conference, Hotel Herradura, San José, 11–15 Aug 2013, *Bat Res News*

IUCN. (2018). IUCN SSC position statement on the culling of the Mauritius Fruit Bat. https://www.iucn.org/sites/dev/files/content/documents/mauritius_bat_position_statement_2018_final.pdf

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.

KARP, D. S., MENDENHALL, C. D., SANDÍ, R. F., CHAUMONT, N., EHRLICH, P. R., HADLY, E. A. & DAILY, G. C. (2013). Forest bolsters bird abundance, pest control and coffee yield. *Ecology Letters*, 16, 1339–1347.

KINGSTON T., FLORENS V., OLEKSY R., RUHOMAUN K. & TATAYAH V. (2018). *Pteropus niger*. The IUCN Red List of Threatened Species 2018: e.T18743A86475525. http://dx.doi.org/10.2305/IUCN.UK.2018-1. RLTS.T18743A86475525.en

KLEIN, A. M., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (2003). Blackwell Publishing Ltd. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology*, 40, 837–845.

KLEIN, A.-M., VAISSIERE, B. E., CANE, J. H., STEFFAN-DEWENTER, I., CUNNINGHAM, S. A., KREMEN, C. & TSCHARNTKE, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc*. B, 274, 303–313. doi:10.1098/ rspb.2006.3721.

KORINE, C., IZHAKI, I. & ARAD, Z. (1999). Is the Egyptian fruit-bat Rousettus aegyptiacus a pest in Israel? An analysis of the bat's diet and implications for its conservation. *Biol Cons*, 88, 301–306.

KUNZ, T. H., DE TORREZ, E. B., BAUER, D., LOBOVA, T. & FLEMING, T. H. (2011). Ecosystem services provided by bats. *New York Academy of Science*. 1223, 1-38. doi: 10.1111/j.1749-6632.2011.06004

LEE, P. C. & PRISTON, N. E. C. (2005). Perception of pests: Human attitudes to primates, conflict, and consequences for conservation. In J. D. Paterson & J. Wallis (Eds.), *Commensalism and conflict: The human-primate interface* (pp. 1–23). Norman, OK: American Society of Primatologists.

LINDEN, B., LINDEN, J., FISCHER, F. & LINSENMAIR, K. E. (2015). Seed dispersal by South Africa's only forest-dwelling guenon, the samango monkey (*Cercopithecus mitis*). *S. Afr. J. Wildl. Res*, 45, 88–99. https://doi.org/10.3957/056.045.0110.

LINDEN, V. M. G., GRASS, I., JOUBERT, E., TSCHARNTKE, T., WEIER, S. M. & TAYLOR, P. J. (2019). Ecosystem services and disservices by birds, bats and monkeys change with macadamia landscape heterogeneity. *Journal of Applied Ecology,* 56, 2069–2078. https://doi.org/10.1111/1365-2664.13424

LIU, P., HUANG, J., CAI, Z., CHEN, H., HUANG, X., YANG, S., SU, Z., AZAM, M., CHEN, H., SHEN, J. (2022). Influence of girdling on growth of litchi (*Litchi chinensis*) roots

during cold-dependent floral induction. *Scientia Horticulturae*, 297, 110928. 10.1016/j.scienta.2022.110928.

LUSKIN, M. S. (2010). Flying foxes prefer to forage in farmland in a tropical dry forest landscape mosaic in Fiji. *Biotropica* 42, 246–250.

MATAA, M. & TOMINAGA, S. (1998). Effects of shading stage and level on fruit set and development, leaf carbohydrates and photosynthesis in Ponkan (*Citrus reticulate* Blanco). *Jpn. J. Trop.Agr*, 42: 103–110.

MCCRACKEN, G. F., WESTBROOK, J. K., BROWN, V. A., ELDRIDGE, M., FEDERICO, P. & KUNZ, T. H. (2012). Bats track and exploit changes in insect pest populations. *PLoS One* 7, e43839. doi:10.1371/journal.pone.0043839.

MELIN, A., ROUGET, M., MIDGLEY, J. & DONALDSON. J. S. (2014). Pollination ecosystem services in South African agricultural systems. *South African Journal Science*,110(11/12). http://dx.doi.org/10.1590/ sajs.2014/20140078.

MINIFIE, G. & WILLI, B. (1990). Duranet cloth and supporting systems. In: Slack JM (ed) Flying fox workshop proceedings, Wollongbar Agricultural Institute, Wollongbar. NSW Agriculture and Fisheries, Australia, pp 47–55.

MUCINA, L. & RUTHERFORD, M. C. (2006). The vegetation of South Africa, Lesotho and Swaziland, Vol. 19. *South African National Biodiversity Institute*, Pretoria.

NAKAMOTO, A., KINJO, K. & IZAWA, M. (2007). Food habits of Orii's flying-fox, *Pteropus dasymallus inopinatus*, in relation to food availability in an urban area of Okinawa-jima Island, the Ryukyu Archipelago, Japan. *Acta Chiropterol*, 9, 237–249.

NEWMAN, E., GOVENDER, K., NIEKERK, S. & JOHNSON, S. (2021). The functional ecology of bat pollination in the African sausage tree *Kigelia africana* (Bignoniaceae). *Biotropica*, 53.

OLEKSY, R. Z., AYADY, C. L., TATAYAH, V., JONES, C., FROIDEVAUX, J. S. P., RACEY, P. A. & JONES, G. (2018). The impact of the Endangered Mauritian flying fox *Pteropus niger* on commercial fruit farms and the efficacy of mitigation. *Oryx*, 55(1), 114-121. https://doi.org/10.1017/50030605318001138

OOSTHUIZEN, J. H. (1993). Recommended cultural practices and research priorities for litchis in South Africa. *South African Litchi Growers' Association Yearbook* 5, 2-5.

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.

SCHOEMAN, P. S. & MOHLALA, R. (2012). Prediction of ideal spraying dates for the stink bug and nut borer complexes. South African Macadamia Association. Yearbook. 20.

SOLOMAKHIN, A. & BLANKE, M. (2007). Overcoming adverse effects of hailnets on fruit quality and microclimate in an apple orchard. *Journal of the science of food and agriculture*, 87, 2625-37. 10.1002/jsfa.3022.

STERN, R. A. & GAZIT, S. (2003). The reproductive biology of the lychee. *Horticultural Previews*. (Janick, J. ed.). John Wiley & Sons Inc., New Jersey, 28, 393-453.

STINGER, S. D., HILL, R. A., SWANEPOEL, L., DALRYMPLE, S. E., LINDEN, B. & KOYAMA, N. F. (2020). Assessing the role of a mammalian frugivorous species on seed germination potential depends on study design: A case study using wild samango monkeys. *Acta Oecologica*, 106, (2020) 103584. https://doi.org/10.1016/j.actao.2020.103584

SYVERTSEN, J. P., GOÑI, C. & OTERO, A. (2003). Fruit load and canopy shading affect leaf characteristics and net gas exchange of 'Spring' navel orange trees. *Tree Physiol*, 23, 899– 906.

TAYLOR, P. J., BOHMANN, K., STEYN, J. N., SCHOEMAN, M. C., MATAMBA, E., ZEPEDA-MENDOZA, M., NANGAMMBI, T. & GILBERT, M. T. P. (2013a). Bats eat pest

green vegetable stinkbugs (*Nezara viridula*): diet analyses of seven insectivorous species of bats roosting and foraging in macadamia orchards at Levubu, Limpopo Province, *South Africa. Southern African Macadamia Growers Association Yearbook* 21, 37–43.

TAYLOR, P. J., MONADJEM, A. & STEYN, J. N. (2013b). Seasonal patterns of habitat use by insectivorous bats in a subtropical African agro-ecosystem dominated by macadamia orchards. *African Journal of Ecology*, 51, 552–561.

THIRIET, D. (2010). Flying fox conservation laws, policies and practices in Australia—a case study in conserving unpopular species. *Australas J Nat Resour Law Policy,* 13:161–194.

TILLMAN, E. A., VAN DOOM, A. & AVERY, M. L. (2000). October. Bird damage to tropical fruit in south Florida. In Wildlife Damage Management Conferences—Proceedings (p. 13).

TINYANE, P. P., SOUNDY, P. & SIVAKUMAR, D. (2018). Growing 'Hass' avocado fruit under different coloured shade netting improves the marketable yield and affects fruit ripening. *Scientia Horticulturae*, 230, 43-49. https://doi.org/10/1016/j.scienta.2017.11.020

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. doi: 10.5061/dryad.5q041fq

ULLIO, L. (2002). To net or not to net that is the question! But is it the answer? In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. R Zool Soc New South Wales, Mosman, NSW, pp 70–76.

WALSH, K. B., GUTHRIE, J. N. & WHITE, D. T. (2006). Control of phytoplasma diseases of papaya in Australia using netting. *Australasian Plant Pathology*, 35, 49–54.

WILLIAMS–GUILLÉN, K., PERFECTO, I. & VANDERMEER, J. (2008). Bats limit insects in a neotropical agroforestry system. Science 320, 70–70.

XIE, J., WANG, J., CHEN, Y., GAO, P., YIN, H., CHEN, S., SUN, D., WANG, W., MO, H., SHEN, J. & LI, J. (2023). Estimating the SPAD of Litchi in the Growth Period and Autumn Shoot Period Based on UAV Multi-Spectrum. *Remote Sensing*, 15, 5767. https://doi.org/10.3390/rs15245767.

ZHANG, W., RICKETTS, T. H., KREMEN, C., CARNEY, K. & SWINTON, S. M. (2007). Ecosystem services and dis-services to agriculture. Ecological Economics, 64, 253–260. https://doi.org/10.1016/j.ecole con.2007.02.024

ZILKAH, S., DAVID, I., LAZAR, M., ROTBAUM, A., ITZHAK, S. & WINER, L. (2013). The effect of high temperature on fruit set of 'Triumph' persimmon. *Acta Horticulturae*, 996, 277–282.

Chapter 5: Summary and practical recommendations

The key contributions of this study are the provision of information and advice to litchi farmers on crop raiding by birds and mammals, fruit bat conservation and potentially promote their ecosystem services of seed dispersal. This study was conducted in both natural habitats of the Soutpansberg and the subtropical fruit growing area of Levubu, Limpopo province, South Africa between February 2018 and December 2020.

Fruit bat perceived damage on agricultural crops has led to a decline in their population and loss of ecosystem services (Aziz *et al*., 2016; Kingston *et al*., 2018; Tollington *et al*., 2019). Fruit bats have a plant-based diet and feed primarily on fruits, nectar, and leaves (Monadjem *et al*., 2020). Pteropodids have been reported to feed on commercial cultivated crops such as litchi, and mango (Fleming *et al*., 2009), causing significant economic damage (Tollington *et al*., 2019). *Rousettus aegyptiacus* are regarded as the main pest in commercial litchi and mango plantations (Jacobsen and du Plessis, 1976; Aziz *et al*., 2016). Bats` ability to feed on variety of plant species aid in the provision of ecosystem service of seed dispersal and forest regeneration (Fujita and Tuttle, 1991; Bonaccorso *et al*., 2014; Abedi-Lartey *et al*., 2016). The perceived damage on commercial fruits has resulted in culling of fruit bats in some parts of the world (Aziz *et al*., 2016). The South African litchi farming industry has reported that colonial (*R. aegyptiacus*) fruit bats raid litchi fruits during the litchi harvest season (Jacobsen *et al*., 1986). Primates, birds, and insects were also reported to cause significant economic damage in litchi orchards. In South Africa, 1 731 ha of land is covered by litchi plantation, with Limpopo especially Levubu area as one of the main producers of litchi (Begemann, 2014). However, most litchi farmers in Levubu have been recently replacing litchi plantation with either macadamia or avocado plantations. The main objective of this study was, thus to gain insight into fruit bats diet, foraging ecology, their ecosystem services and disservices, as well as understanding farmer`s perception towards bats in litchi orchards, South Africa.

Consumption of indigenous wild fruits by fruit bats

Chapter Two showed that epauletted fruit bat diet comprised the highest percentage of wild indigenous fruits of *Ficus* spp. and forest fever tree during the litchi ripe season. Additionally, fruit bat diet in both the agricultural and natural habitats recorded natural figs more than other indigenous fruits. However, *R. aegyptiacus* was never captured in litchi orchards of Levubu, but only a few numbers were captured in the natural habitats in the Soutpansberg. Furthermore, captured *R. aegyptiacus* did not produce any faecal matter nor spit outs for dietary assessment. The litchi-pre ripe season also had the highest percentage of

Ficus spp. and alien exotic fruit (*Melia azedarach*) in the diet of fruit bats. These results suggest that epauletted fruit bats prefer to feed on wild indigenous fruits (Bonaccorso *et al*., 2014; Arumoogum *et al*., 2019; Raji and Downs, 2021) rather than litchi fruits more especially during litchi ripe season, and also target alien exotic fruits (Rollinson *et al*., 2013) during litchi pre-harvest season. Epauletted fruit bats are not opportunistic in their feeding behaviour and do not target ripe litchi orchards in Levubu, unlike to the *R. aegyptiacus* which are colonial roosting in caves and forage in larger groups and respond to the abundance of commercially cultivated fruits such as litchi (Jacobsen and du Plessis, 1976; Jacobsen *et al*., 1986). Since older litchi farmers in Levubu refer anecdotally to nocturnal flocks of bats visiting ripe litchi orchards in the past, it is possible that their unknown cave roost is no longer occupied, explaining why this species was not captured during this study.

The analysis of germination probability between regular seeds (RS) and spit-out seeds (SO), showed higher germination probability by RS when compared to SO, which is opposite what we hypothesized. It is assumed that fruit bats have a positive influence on seed germination, through both mechanical and chemical scarifications of spit-out seeds, which enhances seed germination. Supporting this hypothesis, the lower germination latency by *Ficus* spp. spit-outs corroborates the conclusion that fruit bats have a positive effect on seed germination, and hence a potential ecosystem service provision of seed dispersal. *Ficus* spp. is one of the major wild fruit species consumed and dispersed by epauletted fruit bats, showing improved germination probability and latency in other studies (Snode, 2010; Andrianaivoarivelo *et al*., 2011; de Carvalho-Ricardo *et al*., 2014). The germination trials in this study only compared the germination probability and germination latency between RS and SO. However, future studies should consider the effect of planting of entire fruit, pulp removal, pulp removal plus mechanical scarification of the seed coat, pulp removal plus mechanical and chemical scarification, and gut passage effect plus fertilizer effect from faecal matter on seed germination. Furthermore, a higher sample size and increased sampling effort should also be considered.

Location points from a single GPS-tracked bat (*Epomphorous wahlbergi*) suggested that epauletted fruit bats do not include litchi orchards when foraging during the litchi ripe season but prefer to use semi-natural riparian habitat patches on the border of litchi and macadamia orchards (Appendix E). Although it was based on only a single individual, this result is contrary to other studies on the foraging ecology of fruit bats in relation to ripe litchi orchards (Jacobsen *et al*., 1986; Tollington *et al*., 2019; Attaullah *et al*., 2022). The GPS tracking technique we used in this study was relatively unsuccessful due to the presence of many farm

fences and unfavourable terrains which prevented access to a number of sites. However, radio-tracking which can detect collared bats at a larger distance could produce good results and account for the issue of access (Jacobsen *et al*., 1986; Bonaccorso *et al*., 2014). Perhaps, future studies should consider radio-tracking of bat species from both *Rousettus* and *Epomophorous* genera, in an agricultural matrix dominated by litchi plantation.

The influence of litchi fruiting on species richness and crop raider activity pattern in litchi orchards

This study confirms previous observations in that vertebrates respond to food abundance in agroecosystem (Cleveland *et al*., 2006; Kunz *et al*., 2011; Taylor *et al*., 2013, Gobosho *et al*., 2015; Maurice *et al*., 2019; Findlay and Hill, 2020). The overall species richness (crop raider and incidentally observed species) was increased in response to litchi abundance during litchi ripe season. While crop raiders are known for their opportunistic feeding behaviour in response to food abundance (Lee and Priston, 2005; Maurice *et al*., 2019), camera trap picture analysis in this study suggests lower crop raider species richness compared to incidentally observed species during the litchi harvest season. In contrast to species richness, crop raider abundance was increased during the litchi harvest season. Litchi fruit abundance did not seem to attract more fruit bat crop raider species such as *R. aegyptiacus* as reported by previous studies (Jacobsen *et al*., 1986), but which don't seem to be very abundant in Levubu anymore. Therefore, I suggest a similar study should be conducted in different locations with regular fruit bat crop raiding incidence and higher species diversity.

Dark-capped Bulbuls had the highest RAI when compared to other crop raiders, more especially fruit bats which were thought by farmers to be the main litchi crop raider but, in this study, had a very low RAI. While this confirms previous studies on crop raiding by frugivorous birds' (Patyal and Rana, 2006; Maurice *et al*., 2019), the low RAI of fruit bats may be due to the absence of *R. aegyptiacus* in the area, a known litchi fruit pest species (Jacobsen and du Plessis, 1976; Aziz *et al*., 2016). Crop raiding by Dark-capped Bulbuls, especially in litchi orchards, is understudied. I suggest future studies must focus more on this species` foraging ecology, and diet.

The analysis of seasonal foraging activity patterns of crop raiders` (fruit bats, birds, monkeys), based on the time spent foraging, corroborates the conclusion that annual variation in day length and food availability positively influence the activity of crop raiders. Dark-capped bulbul and Speckled mouse bird, foraged more into nighttime hours in response to litchi fruit abundance during litchi ripe season. Crop raiders` activity pattern is influenced by

seasonal changes (Caravaggi *et al*., 2018) and food availability (Monterroso *et al*., 2014). The results from this study suggested that epauletted fruit bats do not seem to be crop raiders in our study area. Thus, future studies should be conducted at sites where *R. aegyptiacus* is present.

Quantifying ecosystem disservices caused by fruit bats, birds and primates

Another key objective of this study was to quantify the damage caused by fruit bats, birds and primates in litchi orchards using vertebrate exclusion experiments and questionnaire survey.

This study contradicted previous studies showing that exclusion netting reduces damage and increase crop yield in fruit orchards (Tollington *et al*., 2019). The trees inside exclusion cages produced lower yield when compared to paired controls, possibly because excluding insectivorous bats and birds increased insect damage, while higher yields from paired controls might be due to the absence of *R. aegyptiacus*, a known colonial pest species in litchi orchards, capable of causing significant economic impact. At least in these study sites, as a result of these findings, I assume that biological control from insectivorous bats and birds may outweigh the damage from crop raiders.

Fruit bats are perceived to cause significant economic damage in litchi orchards (Aziz *et al*., 2016; Tollington *et al*., 2019). However, results from questionnaire survey of this study revealed that weather and monkeys were perceived as the main cause of damage when compared to fruit bats. These important findings may support the assumption that fruit bats may provide important ecosystem service of seed dispersal, and potential candidate to facilitate forest regeneration.

Practical recommendations and research outlook

The dietary results of this study should incentivize farmers to promote fruit bats conservation, and the maintenance of natural vegetation around orchards to help facilitate seed dispersal of indigenous fruit seeds. Additionally, this will further help in addressing the issue of human-wildlife conflict between litchi farmers and fruit bats which are perceived to raid litchi orchards.

This study also showed that *Ficus* spp. spit-out seeds were enhanced and their germination latency lower than regular seeds. Deriving from this study and the reviewed literature, fruit bats could provide vital ecosystem services and help in habitat restoration (de Carvalho-Ricardo *et al*., 2014; Bonaccorso *et al*., 2014). Additionally, further insight could be gained by improving the germination trial design, which should include germination of whole 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 fertilizer effect from faecal matter (Stinger *et al*., 2020). Improved sampling effort in terms of bat capture, and scouting of more fruit bats roosts, and feeding of captured bats with indigenous fruits in areas where crop raider fruit bat like *R. aegyptiacus* is present, should also be considered by future studies.

The study also showed that natural habitats around orchards are important food sources providing wild indigenous fruits, thus a GPS tracked epauletted fruit bat spent most time foraging over natural habitat and excluding litchi orchards during the ripe litchi season. Previous studies have suggested that epauletted fruit bats prefer wild figs than commercially cultivated fruit and would concentrate their activity around ripe fig trees (Rollinson *et al*., 2013; Bonaccorso *et al*., 2014). However, further insight could be gained by the use of radio tracking, unfortunately accessibility on farms did not allow for radio tracking in this study.

Most studies focus on fruit bats as pest in agroecosystems, rather than their provision of ecosystem services. However, as suggested by Maurice *et al*., (2019), frugivorous birds such as Dark-capped Bulbul and Speckled Mouse bird also cause significant economic damage to fruit and their impact is hardly documented more especially in litchi orchards. The results from this study showed that Dark-capped Bulbuls and Speckled Mouse birds were the most common crop raiders found in litchi orchards, and future studies must focus on these species diet and foraging ecology in relation to litchi orchards.

The crop yield results of this study showed that vertebrate exclusion decreases litchi crop yield and may provide advantage for pest insects which can cause significant damage to the crop. However, previous studies were contradictory to these findings and recorded the opposite results to the current study (Aziz *et al*., 2016; Tollington *et al*., 2019). The perceived damage results also showed weather and monkeys as the main cause of damage compared to the assumed damage by fruit bats. However, the sample size for commercial farmers' questionnaire survey was small (13 respondents), and further insight could be gained by interviewing larger litchi farming community using a face to face method rather than a Google survey form. Future studies must also include assessment of damage signs from both vertebrates and invertebrates.

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. http://dx.doi.org/10.1016/j.gecco.2016.03.005.

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. doi: 10.1515/mamm.2010.071

ARUMOOGUM, 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

ATTAULLAH., 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 (43). https://doi.org/10.1186/s13002-022-00541-9

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*, 377-426. doi:10.1007/978-3-319-25220-9_13

BEGEMANN, G. J. (2014). The South African Litchi Industry – An overview. Acta Horticulturae, 1029, 35-38. https://doi.org/10.17660/ActaHortic.2014.1029.2

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. doi:10.3161/150811014X683255

CARAVAGGI, A., GATTA, M., VALLELY, M-C., HOGG, K., FREEMAN, M., FADAEI, E., DICK, J. T. A., MONTGOMERY, W. I., REID, N. & TOSH, D. G. (2018). Seasonal and

predator-prey effects on circadian activity of free-ranging mammals revealed by camera traps. *PeerJ*, 6: e5827. doi 10.7717/peerj.5827.

CLEVELAND, C. J., BETKE, M., FEDERICO, P., FRANK, J. D., HALLAM, T. G., HORN, J., LOPEZ ´, J. D. JR., MCCRACKEN, G. F., MEDELLÍN, R. A., MORENO-VALDEZ, A., SANSONE, C. G., WESTBROOK, J. K. & KUNZ, T. H. (2006). Economic value of the pest control service provided by Brazilian free–tailed bats in south–central Texas. *Frontiers in Ecology and the Environment* 4, 238–243.

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.

FLEMING, T. H., GEISELMAN, C. & KRESS, W. J. (2009). The evolution of bat pollination – a phylogenetic perspective. *Annals of Botany*, 104, 1017-1043. doi:10.1093/aob/mcp197, available online at www.aob.oxfordjournals.org

FINDLAY, L. J. & HILL, R. A. (2020). Baboon and vervet monkey crop-foraging behaviors on a commercial South African farm: preliminary implications for damage mitigation. *Human–Wildlife Interactions*, 14(3), 505–518.

FUJITA, M. S. & TUTTLE, M. D. (1991). Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology, 5, 455–463.*

GOBOSHO, L., FEYSSA, D. H. & GUTEMA, T. M. (2015). Identification of Crop Raiding Species and the Status of Their Impact on Farmer Resources in Gera, Southwestern Ethiopia. *International Journal of Sciences: Basic and Applied Research,* 22 (2), 66-82.

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 of 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.

KINGSTON T., FLORENS V., OLEKSY R., RUHOMAUN K. & TATAYAH V. (2018). Pteropus niger. The IUCN Red List of Threatened Species 2018: e.T18743A86475525. http://dx.doi.org/10.2305/IUCN.UK.2018-1. RLTS.T18743A86475525.en

KUNZ, T. H., DE TORREZ, E. B., BAUER, D., LOBOVA, T. & FLEMING, T. H. (2011). Ecosystem services provided by bats. *New York Academy of Science*. 1223, 1-38. doi:10.1111/j.1749-6632.2011.06004

LEE, P. C. & PRISTON, N. E. C. (2005). Perception of pests: Human attitudes to primates, conflict, and consequences for conservation. In J. D. Paterson & J. Wallis (Eds.), *Commensalism and conflict: The human-primate interface* (pp. 1–23). Norman, OK: American Society of Primatologists.

MAURICE, M. E., FUASHI, N. A., MENGWI, N. H., EBONG, E. L., AWA, P. D. & DAIZY, N. F. (2019) The Control Methods used by the Local Farmers to reduce Weaver-Bird Raids in Tiko Farming Area, Southwest Region, Cameroon. *Journal of Advanced Studies in Agricultural, Biological and Environmental Sciences*, 6, 2394-2606.

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*, Johannesburg, South Africa. https//dx.doi.org10.18772/22020085829.

MONTERROSO, P., ALVES, P. & FERRERAS, P. (2014). Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: Implications for species coexistence. *Behavioral Ecology and Sociobiology*, 68. 10.1007/s00265-014-1748-1.

PATYAL, S. K. & RANA, R. S. (2006). Bird damage to kinnow fruits in Himachal Pradesh and evaluation of management techniques against them. Pest Management and Economic Zoology, 14, 157-161.

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

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. *African Zoology*, 48 (2), 340-350. doi:10.3377/004.048.0218

SNODE, 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

STINGER, S. D., HILL, R. A., SWANEPOEL, L., DALRYMPLE, S. E., LINDEN, B. & KOYAMA, N. F. (2020). Assessing the role of a mammalian frugivorous species on seed germination potential depends on study design: A case study using wild samango monkeys. *Acta Oecologica*, 106, (2020) 103584. https://doi.org/10.1016/j.actao.2020.103584

TAYLOR, P. J., BOHMANN, K., STEYN, J. N., SCHOEMAN, M. C., MATAMBA, E., ZEPEDA-MENDOZA, M., NANGAMMBI, T., & GILBERT, M. T. P. (2013). Bats eat pest green vegetable stinkbugs (*Nezara viridula*): diet analyses of seven insectivorous species of bats roosting and foraging in macadamia orchards at Levubu, Limpopo Province, *South Africa. Southern African Macadamia Growers Association Yearbook*, 21, 37–43.

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. doi:10.5061/dryad.5q041fq

Appendices

Appendix A. Table showing localities for captured bats and spit out collection sites in the Vhembe Biosphere Reserve.

Locality	Lat.	Long.	Time of sampling	Land use
Bergplaats Research Camp	-23.04	29.44	In and out of litchi harvest	Soutpansberg Mountain Bushveld
Goro Game Reserve	-22.98	29.43	Out of litchi harvest	Soutpansberg Mountain Bushveld
Lajuma Research Centre	-23.03	29.44	Out of litchi harvest	Soutpansberg Mountain Bushveld
Laatsgevonden (Levubu)	-23.08	30.34	In and out of litchi harvest	Litchi, Guava, Mango, and Macadamia orchards
Itsani tower	-23.01	30.41	Out of litchi harvest	Residential
Makumbane Farming Enterprise	-22.59	30.22	Litchi harvest	Litchi orchards
Sigurwana	-22.59	29.28	Litchi harvest	Soutpansberg Mountain Bushveld
Tshitwani Fruit Farm	-23,07	30,33	Litchi harvest	Litchi orchards
van Wyk	-23,08	30,32	Litchi harvest	Avocado, Litchi and Banana orchards

Appendix B. Fruit bats capture data showing individual locality, day of capture, morphometric data, surrounding area and food remains from faecal matter and spit outs.

Locality	Date	Bat species	Gender	Mass (g)	Forearm length (mm)	Surrounding area	Food remains identified
Goro Game Reserve	20/02/2018	*E. wahlbergi*	Female	87	84.23	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	*Ficus* seeds from bat faecal matter and spit outs (remains from cheek pouches and fur)
Bergplaats Research Camp	14/09/2018	*E. wahlbergi*	Male	94	90	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	19/09/2018	*E. wahlbergi*	Male	114	84	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	*Ficus* seeds from bat faecal matter
Bergplaats Research Camp	29/10/2018	*E. wahlbergi*	Female	100	82.3	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	29/10/2018	*E. wahlbergi*	Female	74	77.63	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	29/10/2018	*E. wahlbergi*	Female	90	82.14	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	*Ficus* and *A. grandiflora* seeds from bat faecal matter
Bergplaats Research Camp	29/10/2018	*E. wahlbergi*	Female	73	73.4	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	29/10/2018	*E. wahlbergi*	Female	108	82.04	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	*Ficus* and *A. grandiflora* seeds from bat faecal

							matter
Bergplaats Research Camp	29/10/2018	*E. wahlbergi*	Male	105	87.7	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	30/10/2018	*E. wahlbergi*	Male	123	85.7	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	*Ficus* seeds from bat faecal matter
Bergplaats Research Camp	22/01/2019	*E. wahlbergi*	Male	105	82.67	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	22/01/2019	*R. aegyptiacus*	Male	66	77.56	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	22/01/2019	*E. wahlbergi*	Male	118	85.45	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	*Ficus* seeds from bat faecal matter
Bergplaats Research Camp	22/01/2019	*R. aegyptiacus*	Male	80	79.52	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	23/01/2019	*R. aegyptiacus*	Female	65	73.62	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Bergplaats Research Camp	23/01/2019	*E. wahlbergi*	Female	63	75.82	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	*Ficus* seeds from bat faecal matter
Bergplaats Research Camp	23/01/2019	*R. aegyptiacus*	Male	93	81.33	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Laatsgevonden (Levubu)	11/06/2019	*E. crypturus*	Female	90	73	Litchi, Guava, Mango, and Macadamia orchards	None
Laatsgevonden (Levubu)	12/06/2019	*E. crypturus*	Male	112	81	Litchi, Guava, Mango, and Macadamia orchards	None

Laatsgevonden (Levubu)	12/06/2019	*E. crypturus*	Male	111.5	84.9	Litchi, Guava, Mango, and Macadamia orchards	None
Laatsgevonden (Levubu)	12/06/2019	*E. crypturus*	Female	30	65.5	Litchi, Guava, Mango, and Macadamia orchards	*Ficus* seeds from bat faecal matter
Laatsgevonden (Levubu)	12/06/2019	*E. crypturus*	Female	93	81.5	Litchi, Guava, Mango, and Macadamia orchards	*Ficus* seeds from faecal matter and *P. guajava* seeds from spit out (half fruit in the mouth)
Bergplaats Research Camp	25/06/2019	*E. wahlbergi*	Female	93	85	Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006)	None
Laatsgevonden (Levubu)	17/10/2019	*E. crypturus*	Male	113	85.5	Litchi, Guava, Mango, and Macadamia orchards	*Ficus* seeds from bat faecal matter
Laatsgevonden (Levubu)	17/10/2019	*E. crypturus*	Male	137	80.4	Litchi, Guava, Mango, and Macadamia orchards	*Ficus* seeds from bat faecal matter
Laatsgevonden (Levubu)	17/10/2019	*E. crypturus*	Male	80	75.5	Litchi, Guava, Mango, and Macadamia orchards	*A. grandiflora* seeds from bat faecal matter
Laatsgevonden (Levubu)	17/10/2019	*E. wahlbergi*	Male	111	80.6	Litchi, Guava, Mango, and Macadamia orchards	Unidentified yellow pulp from bat faecal matter
Laatsgevonden (Levubu)	24/10/2019	*E. wahlbergi*	Female	74	78	Litchi, Guava, Mango, and Macadamia orchards	None
Laatsgevonden (Levubu)	17/10/2019	*E. wahlbergi*	Male	132	86	Litchi orchards	*Ficus* seeds from bat faecal matter
Laatsgevonden (Levubu)	29/10/2019	*E. wahlbergi*	Female	86	79.5	Litchi, Guava, Mango, and Macadamia orchards	None
Laatsgevonden (Levubu)	30/10/2019	*E. wahlbergi*	Female	84	75.5	Litchi, Guava, Mango, and Macadamia orchards	*Ficus* seeds from bat faecal matter
van Wyk (Levubu)	23/12/2019	*E. crypturus*	Male	117	84.55	Avocado, Litchi and Banana orchards	*Ficus* seeds from bat faecal matter

Van Wyk (Levubu)	23/12/2019	*E. crypturus*	Male	111	80.1	Avocado, Litchi and Banana orchards	*A. grandiflora* seeds from faecal matter
Laatsgevonden (Levubu)	31/10/2020	*E. wahlbergi*	Male	82	76.3	Litchi, Guava, Mango, and Macadamia orchards	Unidentified yellow pulp from bat faecal matter
Laatsgevonden (Levubu)	31/10/2020	*E. crypturus*	Male	88	76.2	Litchi, Guava, Mango, and Macadamia orchards	None
Tshitwani Fruit Farm	04/11/2020	*E. wahlbergi*	Female	88	70.3	Litchi orchards	*A. grandiflora* seeds from bat faecal matter and spit outs (remains from cheek pouches and fur)
Tshitwani Fruit Farm	04/11/2020	*E. wahlbergi*	Male	118	89	Litchi orchards	*A. grandiflora* seeds from bat faecal matter and spit outs (remains from cheek pouches and fur)
Tshitwani Fruit Farm	04/11/2020	*E. wahlbergi*	Female	79	70.1	Litchi orchards	*A. grandiflora* seeds from bat faecal matter
Tshitwani Fruit Farm	04/11/2020	*E. wahlbergi*	Male	129	82.2	Litchi orchards	*Ficus* and *A. grandiflora* seeds from bat faecal matter and spit outs (remains from cheek pouches and fur)
Tshitwani Fruit Farm	04/11/2020	*E. wahlbergi*	Male	129	87	Litchi orchards	*Ficus* seeds from bat faecal matter
Tshitwani Fruit Farm	04/11/2020	*E. crypturus*	Female	89	80	Litchi orchards	*Ficus* seeds from bat faecal matter
Tshitwani Fruit Farm	22/11/2020	*E. wahlbergi*	Male	113	84	Litchi orchards	None

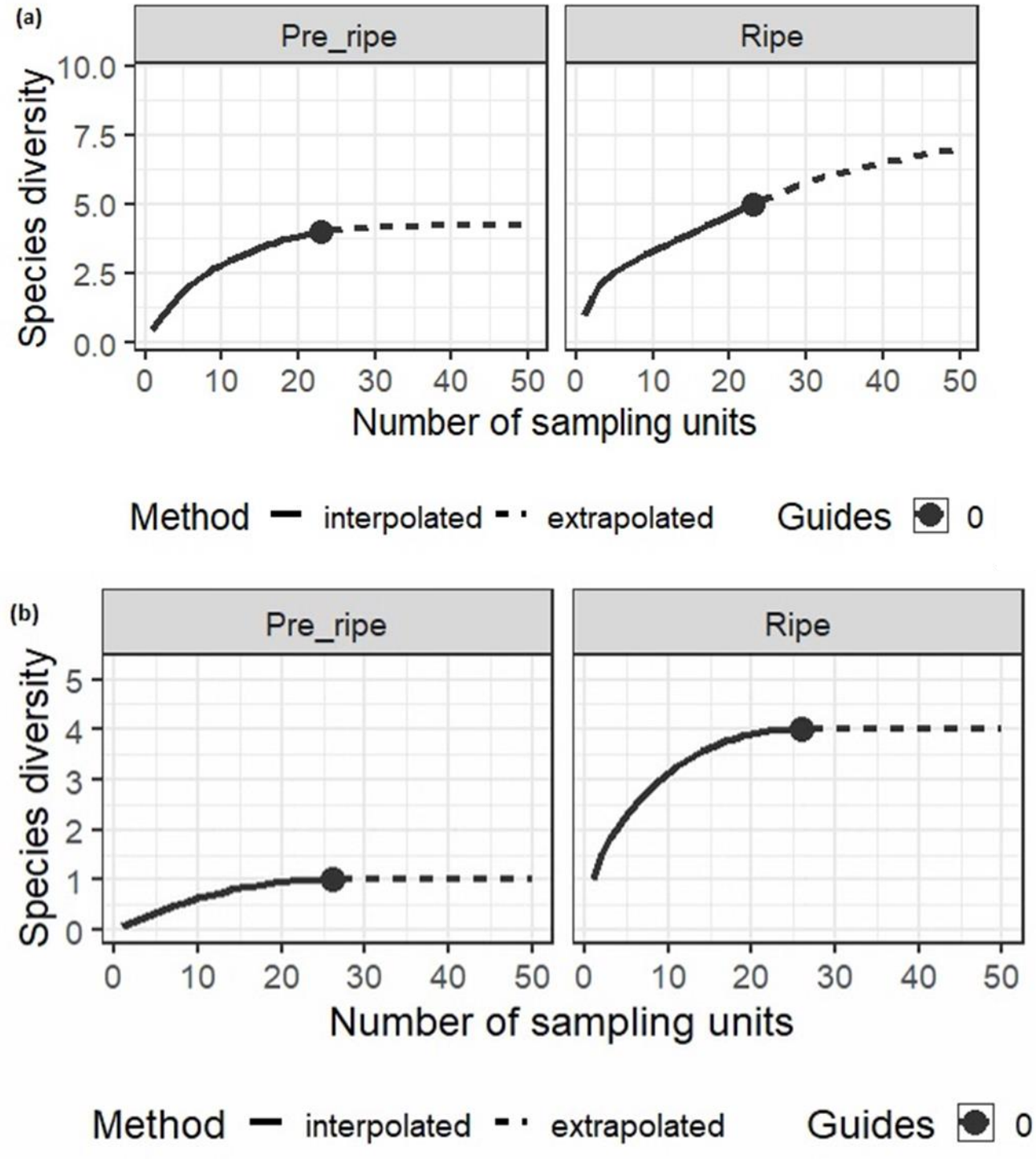
Tshitwani Fruit Farm	22/11/2020	*E. crypturus*	Male	115	84.5	Litchi orchards	*Ficus* seeds from bat faecal matter
Tshitwani Fruit Farm	22/11/2020	*E. crypturus*	Male	109	86	Litchi orchards	*Ficus* and *A. grandiflora* seeds from bat faecal matter
Tshitwani Fruit Farm	22/11/2020	*E. crypturus*	Male	99	81	Litchi orchards	*Ficus* and *A. grandiflora* seeds from bat faecal matter and spit outs (remains from cheek pouches and fur)
Tshitwani Fruit Farm	22/11/2020	*E. wahlbergi*	Male	119.5	85	Litchi orchards	*Ficus* seeds from bat faecal matter
Tshitwani Fruit Farm	26/11/2020	*E. crypturus*	Male	113.5	82	Litchi orchards	None
Tshitwani Fruit Farm	26/11/2020	*E. crypturus*	Male	103	75	Litchi orchards	None
Tshitwani Fruit Farm	26/11/2020	*E. wahlbergi*	Female	78	65	Litchi orchards	None

Appendix C. Summary of GPS collaring dates, search effort, and number of recorded points (GPS position) for the four fruit bats during litchi season in the Levubu Laatsgevonden area (farm Laatsgevonden, Tshitwani Fruit Farm and van Wyk`s farmhouse).

Location	**GPS collaring date**	**Species**	**Gender**	**Search effort**	**Number of recovered points**
Laatsgevonden	24/10/2019	*E. wahlbergi*	Female	EP BS-P5 base station with omnidirectional antenna was mounted on a 3m flagpole and mist nets deployed for 6 hours. The base station was also mounted on vehicle roof during drive transects. The collared bat was picked by the base station on the fourth night after capture (28/10/2019), and it was never picked up again nor caught in mist nets despite considerable search throughout November and December 2019. The orchards were also searched for GPS logger which might have dropped during flight, but nothing was recovered.	48
Farmhouse (van Wyk)	24/12/2019	*E. crypturus*	Male	Despite considerable search with the base station (driving around and mounting base station on a Lapa below roost) and ground search for dropped GPS logger from 24/12/2019 until the second week of January, the collared bat was never	0

				picked up nor logger recovered, and until today the bats have since vacated the palm tree roost at the farmhouse.	
Farmhouse (van Wyk)	24/12/2019	*E. crypturus*	Male	The collared bat was picked by the base station but produced a NO SAT error message with no GPS points. Considerable search continued from the collaring date until the second week of January and no GPS logger was recovered neither picked by the base station. Fruit bats were reported to have vacated the palm tree roost since day of capture.	0
Tshitwani Fruit Farm	26/11/2020	*E. crypturus*	Male	Despite considerable search with base station, mist nets, and orchards search for dropped GPS logger from the date of capture until the first week of January 2021, nothing was picked by the base station nor GPS logger recovered from the ground.	0

Appendix D. Sample rarefaction curves showing sample completeness for (a) farm habitat at Levubu during pre-ripe and ripe litchi season and (b) natural area pre-ripe and ripe seasons.



Appendix E. Supplementary map showing GPS records from a single tracked female *Epomophorous wahlbergi* (24-28 October 2019) during ripe litchi season in the Levubu Laatsgevonden farming area. From the 9 tree species recorded in the Levubu Laatsgevonden area 3 indigenous fruit species (*Anthocleista grandiflora*, *Ficus* spp. and *Rauvolfia caffra*) and 2 commercial fruit species (*Litchi chinensis* and *Mangifera indica*) were fruiting during ripe litchi season. However, *Syzygium cordatum* was flowering and *Melia azedarach*, *Parinari curatellifolia and Psidium guajava* didn't have flowers nor any sign of fruits. The white patches are abandoned farms due to land claims, which were used to cultivate guava, mango, and banana fruits**.**

Appendix F. Blank copy of questionnaire survey used to interview commercial (online) and small-scale farmers (face to face).

Survey Questionnaire (Fruit bat damage assessment on Litchi farms)

PhD study at the University of Venda, Department of Biological Sciences, Faculty of Science, Engineering and Agriculture

PERSONAL DETAILS

Name and Surname

_____

Gender

- ◯ Male
- ◯ Female
- ◯ Other

Age

_____

Are you the owner or manager?

- ◯ Owner
- ◯ Manager
- ◯ Other

How many years are you living on the farm?

_____

Home language

_____

Name of the farm

_____

Farm location

_____

How many hectares of land do you own or manage?

_____

Which crops are grown on the farm?

_____

FARM CHARACTERISTICS

(Please roughly estimate for your farm)

Percentage of land under litchi plantation (%)

_____

Percentage of land under other tree crops (%)

_____

Percentage of land under natural forest cover (%)

_____

Percentage of land under river ways or water bodies (%)

_____

What is your total litchi income per annum?

- ◯ Less than R10 000
- ◯ R10 500 – R25 000
- ◯ R25 500 – R75 000
- ◯ R75 500 – R100 00
- ◯ More than R100 000

Do you have other potential income streams?

- ◯ Macadamia
- ◯ Avocado
- ◯ Mango
- ◯ Other

If yes, please specify the annual income of other crops (%)

_____

FRUIT BAT DAMAGE

How often do fruit bats raid litchi orchards during fruiting season?

- ◯ Every night
- ◯ Once in two nights
- ◯ Twice a week
- ◯ Other

Which litchi variety is more susceptible to fruit bat damage?

- ◯ Mauritius cultivar
- ◯ Chinese cultivar
- ◯ Madras cultivar

- ◯ No difference

What is the relative number of litchi skin found in the orchard during fruiting season?

- ◯ Plentiful in most orchards
- ◯ Commonly observed in some orchards
- ◯ Never seen

How much (in kg) litchis do you harvest per annum?

_____

How much (% of your total harvest) do you think is damaged by fruit bats?

_____

How much (% of your total harvest) do you think is damaged by insects?

_____

How much (% of your total harvest) do you think is damaged by birds?

_____

How much (% of your total harvest) do you think is damaged by weather (sun/rain)?

_____

How much (% of your total harvest) do you think is damaged by monkeys?

_____

Can you think of any other source of damage? If yes, please specify

_____

_____

_____

CONTROL METHODS

How often do you meet experts to get advice or help on controlling fruit bat damage?

- ◯ Before fruiting season
- ◯ During fruiting season
- ◯ Never

Which method do you use to protect your litchi trees from animal damage?

- ◯ Pesticides
- ◯ Litchi bags or nets
- ◯ Poison
- ◯ Shooting
- ◯ Farm patrol/patrol dogs
- ◯ Other

Do you feel it is effective?

_____

What animal (s) do you target for pest control?

_____

What are your estimated annual costs for using this control method?

_____

FRUIT BAT PERCEPTION AND NATURE

How do you feel towards bats and other animals?

_____

_____

_____

_____

Do you feel you know much about the ecosystem services fruit bats provide to the environment?

- ◯ Yes
- ◯ No
- ◯ Other

What would be the most successful method to control bats?

- ◯ Netting
- ◯ Shooting
- ◯ Decoy crops (non-commercial fruits which are more attractive to bats)
- ◯ Biological agents (weaver ants)
- ◯ Deterrents/aversion agents (smoke, rotating lights, electronic distress sounds e.t.c)

Why do you think this is the most successful method?

_____

_____

_____

_____

Is there anything else you would like to tell me?

_____

_____

_____