Extent of damage to commercial fruits by a *Pteropus* species varies through a single night and through the fruiting season offering new prospects to mitigate human-wildlife conflicts

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Human-wildlife conflicts (HWC) pose a growing threat to biodiversity particularly when the targeted species plays an ecological keystone role. Mauritius has repeatedly mass-culled a Mascarenes endemic and threatened flying fox species without reaching intended objectives making the species more threatened. In this context it is important to devise non-lethal alternatives that would work both for planters and conservation. Consequently, the foraging ecology of the flying fox needs to be better understood if non-lethal management is to be devised and optimized. Here we investigate foraging patterns of vertebrate frugivores over 24 hours cycles in lychee orchards and backyard gardens. We assessed all agents of damage (mainly bat, alien bird, alien mammal) to fruits sampled in 2022, and particularly the temporal variation of bat and bird foraging (take and amount eaten relative to fruit ripeness) on lychee trees at six-hourly intervals. We sampled two orchards and three backyard gardens during six-hourly periods using 120 permanent fruit traps. There was no significant difference between the number of fruits eaten by bat before and after midnight at one orchard, but fewer fruits were destroyed after midnight at the other. Fruits from backyard trees sustained more bat damage in early than late night. Bird damage at both orchards was higher during the first half of the day. As lychees ripen, the proportion of flesh eaten per fruit by bat and bird increased. The number of fruits lost to alien mammals (0.1%) was negligible compared to fruits lost to birds (16.1%) and bats (78.3%). Other form of damage accounted for 5.4%. Deliberate disturbances in orchards (deterrent methods involving smoke, noise or light to repulse bats) may influence the foraging behaviour of fruit bats especially when such deterring activities are more concentrated during early nights. The backyard trees assessed were left undisturbed and hence are deemed to reflect the natural behaviour of the bats better. The foraging activity of birds peaked between sunrise and midday. The results also show that bats and birds eat both unripe and ripe fruits, with preference for latter, which would also increase animals' satiation as a greater proportion of the riper (and larger) fruits are consumed. This study quantifies fruit damage partitioning between diurnal and nocturnal species, permitting a precise knowledge of the extent of damage done by frugivores through time on a daily and nightly basis and throughout the lychee season. Optimization of active deterrence methods in orchards can occur both on a nightly level (concentrating on earlier night) and seasonal level (concentrating on earlier season) for bat, and on early morning for bird. Hence, this equips managers with improved knowledge of temporally-responsive active deterrence action that should produce higher returns per unit of investment thereby contributing towards alleviating the HWC between fruit growers and fruit bats.

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Abstract

Human-wildlife conflicts (HWC) pose a growing threat to biodiversity, particularly when the targeted species plays an ecological keystone role. Mauritius has repeatedly mass-culled a Mascarenes endemic and threatened flying fox species without reaching intended objectives, making the species more threatened. In this context it is important to devise non-lethal alternatives that would work both for planters and conservation. Consequently, the foraging ecology of the flying fox needs to be better understood if non-lethal management is to be devised and optimized. Here we investigate foraging patterns of vertebrate frugivores over 24 hours cycles in lychee orchards and backyard gardens. We assessed all agents of damage (mainly bat, alien bird, alien mammal) to fruits sampled in 2022, and particularly the temporal variation of bat and bird foraging (take and amount eaten relative to fruit ripeness) on lychee trees at six-hourly intervals. We sampled two orchards and three backyard gardens during six-hourly periods using 120 permanent fruit traps. There was no significant difference between the number of fruits eaten by bat before and after midnight at one orchard, but fewer fruits were destroyed after midnight at the other. Fruits from backyard trees sustained more bat damage in early than late night. Bird damage at both orchards was higher during the first half of the day. As lychees ripen, the proportion of flesh eaten per fruit by bat and bird increased. The number of fruits lost to alien mammals (0.1%) was negligible compared to fruits lost to birds (16.1%) and bats (78.3%). Other form of damage accounted for 5.4%. Deliberate disturbances in orchards (deterrent methods involving smoke, noise or light to repulse bats) may influence the foraging behaviour of fruit bats especially when such deterring activities are more concentrated during early nights. The backyard trees assessed were left undisturbed and hence are deemed to reflect the natural behaviour of the bats better. The foraging activity of birds peaked between sunrise and midday. The results also show that bats and birds eat both unripe and ripe fruits, with preference for latter, which would also increase animals' satiation as a greater proportion of the riper (and larger) fruits are consumed. This study quantifies fruit damage partitioning between diurnal and nocturnal species, permitting a precise knowledge of the extent of damage done by frugivores through time on a daily and nightly basis and throughout the lychee season. Optimization of active deterrence methods in orchards can occur both on a nightly level (concentrating on earlier night) and seasonal level (concentrating on earlier season) for bat, and on early morning for bird. Hence, this equips managers with improved knowledge of temporally-responsive active deterrence action that should produce higher returns per unit of investment thereby contributing towards alleviating the HWC between fruit growers and fruit bats.

Introduction

Human-wildlife conflict (HWC) arises when human goals are negatively impacted by the needs and behaviour of wildlife or vice versa (Madden, 2004), for instance, when wildlife is posing a threat to human safety or damaging crops leading to human retaliation (Warne & Jones, 2003; Peterson et al., 2010; Florens, 2016). Such conflicts are considered as a serious and growing challenge faced by wildlife (Frank, Glikman & Marchini, 2019). These conflicts, especially in anthropogenic landscapes like agricultural areas (König et al., 2020), are expected to worsen globally (Dickman, 2010; Seoraj-Pillai & Pillay, 2016) as human population size, consumption rates and rates of habitat destruction progress (Ripple et al., 2017, 2020, 2021). This is particularly problematic when the species at the centre of the conflict plays an ecological keystone role (Florens et al., 2017) especially where other species playing similar roles have been driven extinct by human activities (Cheke & Hume, 2008) and where species introduced by humans cannot fulfil that role adequately (Heinen et al., 2023). Hence, to address these conflicts, there is an increasing need for novel multi-disciplinary strategies (White & Ward, 2010), focusing on evidence-based approaches (e.g. Florens and Baider, 2019; Siex and Struhsaker, 1999).

Flying foxes forage on commercial crops worldwide (Aziz et al., 2016) leading to HWC and frequently resulting in persecution, illegal killing (Kingston, Florens & Vincenot, 2023) or legal culling (Bumrungsri et al., 2009; Epstein et al., 2009; Florens, 2016). While non-lethal alternatives to protect fruit trees such as netting (Korine, Izhaki & Arad, 1999; Oleksy et al., 2021) or using deterrent systems (Ullio, 2002; Chakravarthy & Girish, 2003) are common, certain perceptions or difficulties may impede their full implementation such as high costs, labour intensiveness and time they take to be implemented (Gough, 2002; Ullio, 2002; Tollington et al., 2019). In this context, an improved understanding of the bat's foraging ecology like peak foraging time and foraging behaviour related to human presence and movement ecology is crucial to better devise and optimise non-lethal alternatives that could potentially alleviate HWC (Verghese, 1998; Srinivasulu & Srinivasulu, 2002; Hengjan et al., 2018; Schloesing et al., 2020).

Mauritius appeared in the HWC literature when it started planning mass-culling a species threatened with extinction (Florens, 2012) - the Mauritian flying fox (*Pteropus niger*) - because it includes commercial fruits like lychee (*Litchi chinensis* Sonn., Sapindaceae) and mango (*Mangifera indica* L., Anacardiaceae) in its diet (Tollington et al., 2019; Oleksy et al., 2021). *Pteropus niger* is a Mascarene endemic (Cheke & Hume, 2008) ecological keystone species (Florens et al., 2017), a role amplified due to human-driven frugivore extinctions (Albert et al., 2021; Heinen et al., 2023) and was already threatened before the mass-culling campaigns (Hutson & Racey, 2013). As claims of damage to commercial fruits increased from 30-40% in 2012, 73% in 2014 to 75-100% in 2015 (Government of Mauritius, 2010; Anon., 2013, 2015a,b), the government weakened the country's main biodiversity protection law in November 2015 to enable mass-culling of bats (Florens, 2015, 2016). Repeated mass-culling campaigns (Olival, 2016; Vincenot, Florens & Kingston, 2017; Florens & Vincenot, 2018; Chelvan, 2020) ensued and contributed to the worsening of *P. niger*'s International Union for Conservation of Nature (IUCN) Red List category (from Vulnerable to Endangered) (Kingston et al., 2018). As scientists predicted, mass-culling was ineffective in increasing fruit production (Olival, 2016; Florens & Baider, 2019). Previous studies have investigated temporal variation of *P. niger* movements at a broad island-wide scale in forested and cultivated areas (Oleksy et al., 2019; Seegobin, Oleksy & Florens, 2022), but none have investigated the temporal variation in fruit consumption by vertebrate frugivores in anthropogenic landscapes.

The mitigation or resolution of HWC depends in part on a good understanding of the agents causing discontent and on temporal expressions of the undesired effects. Consequently, we investigated the foraging patterns of vertebrate frugivores over 24 hours cycles in lychee orchards and backyard gardens in Mauritius to 1) assess the contribution of different agents to fruit damage; 2) evaluate patterns in vertebrate frugivores' foraging behaviour; and 3) explore the effect of fruit ripeness on foraging behaviour of the vertebrate frugivores. We hypothesise that temporal patterns of foraging by frugivores would exist that may be useful to improve the efficacy of active non-lethal deterrence. Specifically, we hypothesised that bats would more likely target quick sugar resources (like lychee) during early nights after their day-time fast. Similarly, we hypothesised that birds that include fruits in their diet, would seek eating more fruits in the morning after their night-time fast to replenish energy levels. We also predict that the amount of commercial fruit eaten by bats would differ before and after midnight (Seegobin, Oleksy & Florens, 2022) and throughout the fruiting season as ripeness of fruits progressively increases, increasing the fruits' attractiveness to frugivores. We finally hypothesise that foraging decisions of frugivores are associated with knowledge on spatio-temporal cues (Crestani, Mello

& Cazetta, 2019; Trapanese, Meunier & Masi, 2022), and predict that amount of fruit eaten by bats and birds increases with increasing fruit-ripeness. We then discuss how our findings could help improve non-lethal alternatives in the interest of fruit growers and biodiversity.

Materials & Methods

Site and species description

Mauritius (20°20′S; 57°34′E) is a volcanic island of 7.8 M years old in the Indian Ocean about 900 km east of Madagascar (Fig. 1). It covers 1,865 km^2, spanning about 60 x 40 km, has a maximum elevation of 828 m and is located within one of the world's biodiversity hotspots (Myers et al., 2000). The mean annual temperature is 22 °C and the mean annual rainfall varies from 800-4,000 mm (Staub, Stevens & Waylen, 2014). Habitat destruction due mainly to agriculture and urban development decreased its native forest cover to 4.4% (Hammond et al., 2015). Sugarcane plantations have occupied more than 50% of Mauritius (Nigel, Rughooputh & Boojhawon, 2015). However, land under sugarcane plantations is being converted to other crops including fruit crops (Ministry of Agro-Industry and Food Security, 2015). Lychee is one of the three main fruits produced on the island (Statistics Mauritius, 2017), and it has economic importance to both the local market (around 7,000 tonnes) and export industry (around 1,000 tonnes) (Fresh Plaza, 2016).

The Mauritian flying fox is a medium-sized fruit bat of 380-540 g and the last *Pteropus* species surviving on Mauritius following the extinction of two other species from the island (Cheke & Hume, 2008). Its natural diet consists of leaves, nectar, flowers and mainly a wide variety of native fruits, making this species a keystone seed disseminator (Florens et al., 2017) and a potential pollinator (Nyhagen et al., 2005). Following the extinction of the two other *Pteropus* species, giant tortoises, the dodo and other large frugivores, *P. niger* has become the largest native seed disseminator of the island and of the Mascarenes (Hansen & Galetti, 2009; Heinen et al., 2023). It is known to be able to cross the whole island in a single night for foraging (Oleksy et al., 2019).

Sampling and statistical analyses

We selected two lychee orchards, one at Calebasses (north, nine hectares) and one at Beaux Songes (west, seven hectares) and backyard gardens in the north and central uplands region (Fig. 1). Twelve non-netted unharvested fruiting trees of ~eight m height and nine-11 m canopy diameter were randomly selected in each orchard and six trees were selected in backyards. Permanent quadrats of 1 m^2 were placed at the four cardinal points, under the canopy of each assessed tree. We assessed all agents of vertebrate frugivore damage (bat, bird, rat and long-tailed macaque) according to bite marks of fruits (Fig. 2) sampled every six hours (06:00-12:00, 12:00-18:00, 18:00-00:00, 00:00-06:00) for 24-hour cycles between 12 November to 27 December 2022. Data was collected for three consecutive cycles per week until no fruits remained on the tree. We also collected data on the amount of flesh eaten by each frugivore on individual fruits and their corresponding ripeness. Amount of flesh eaten and fruit ripeness (characterised by change in pericarp colour from green to red) were both categorised into percentages (0%, 25%, 50% and 100%) (Fig. S1). Data collected for backyard trees was focused on temporal quantification of bat damage only. We also randomly selected 42 ripe fruits from a backyard tree and measured their weight to the nearest 0.01 g. We installed one AudioMoth (recording 55 seconds every five minutes from 18:00-06:00) for two consecutive weeks in each orchard to record the presence of any deliberate disturbance made to deter bats.

All statistical analyses were conducted in R (version 4.3.1) (R Core Team 2023). Analyses were done for bats and birds only as we had too few observations for rats and macaques. We tested the hypothesized effects of cycle (sampled days) and time slot (06:00 – 12:00, 12:00 – 18:00, 18:00 – 00:00 and 00:00 – 06:00) on the amount of fruits eaten by birds and bats per tree in every site (Beaux Songes and Calebasses for both animals, and also backyards for bats) using Generalized Linear Models (GLMMs) with negative binomial error distributions. We first fitted global models (using package glmmTMB (Magnusson et al., 2024)) with two-way interactions between cycle and site and between time slot and site, to account for within-site variation in the relationships between fruits eaten, time slot and cycle. For bats, we only included two time slots (18:00 – 00:00 and 00:00 – 06:00), as they almost exclusively fed during these time slots. For birds we included all time slots, as they usually started feeding before 06:00 and finished feeding after 18:00. We included tree as random effect to account for correlation of repeated measurements per tree across time (Harrison, 2014). We evaluated model fit of all global models using residual diagnostic plots from package DHARMa (Hartig, 2022).

We used the global model for inference, as this also provides a balanced representation of statistically non-significant results. We first tested the global model against a null model with a likelihood ratio test (Forstmeier & Schielzeth, 2011). Next, we reported the model estimates and evaluated statistical significance of observed estimates using 95% confidence intervals (CIs) (Nakagawa & Cuthill, 2007). We considered evidence for an effect as weak, moderate and strong when the 90, 95 and 99% CIs did not overlap zero, respectively (Muff et al., 2022). For the two-way interaction between site and cycle in each GLMM, we calculated regression coefficients, standard errors (SEs), and CIs for the cycle slope for site, correcting for multiple comparisons using the Tukey method (package emmeans (Lenth et al., 2017)). For the two-way interaction between site and time slot in each GLMM, we carried out post hoc contrast tests for the pairwise comparisons between time slots in every site (using package emmeans).

We also tested our hypothesised effects of stage of fruit ripeness on the proportion of flesh eaten by different animals (bat, parakeet or other birds) in each orchard (Beaux Songes and Calebasses) using a GLMM with ordered β distribution (and using individual fruits as sampling units). The ordered β distribution is similar to the zero-one-augmented β distribution (recommended for continuous proportions) (Douma & Weedon, 2019) but produces more accurate estimates and needs less processing time (Kubinec, 2023). In this GLMM, we included a three-way interaction between site, animal and fruit ripeness stage and between site, animal and cycle as fixed effects. We also included tree as a random effect to account for pseudoreplication. We used the same validation procedures as described for the previous GLMMs and used the global model for inference. We calculated regression coefficients, standard errors (SEs) and CIs for the slope of fruit ripeness stage for every animal in every site and carried out post hoc contrast tests for the pairwise comparisons between predicted means in proportion of flesh eaten by different animals for different stages of fruit ripeness in every site.

Results

Agents of fruit loss

Fruit loss by frugivores in orchards was caused by bats (native) and birds, rats and macaques (all alien). We also accounted for fruit loss by other factors which included mainly fungal diseases, fruit cracking and natural fruit fall. At Calebasses and Beaux Songes respectively, fruit loss averaged 71.6±5.8% and 85.1±9.4% caused by bats; 22.7±5.3% and 9.5±6.8% caused by introduced birds; and 5.7±3.1% and 5.2±3.0% caused by other factors at. Rats and macaques combined accounted for less than 1% fruit loss and it occurred at Beaux Songes orchard only. We identified four alien bird species feeding on lychees namely the ring-necked parakeet (*Alexandrinus krameri*), red-whiskered bulbul (*Pycnonotus jocosus*), village weaver (*Ploceus cucullatus*) and common myna (*Acridotheres tristis*). The highest damage frequency of all sampled fruits was by bats (n=446) and birds (n=306) and the lowest was for rats (n=3) and macaques (n=1). Hence, bats and birds were classified as regular visitors while rats and macaques were considered occasional visitors.

Bat foraging behaviour and temporal pattern

We found strong evidence that flying foxes eat more fruit before than after midnight in Beaux Songes orchard and in backyards. They eat less fruits towards the end of the study in both orchards (Table 1, Fig. 3). The low R^2_{marginal} indicated that our predictors only explained 11% of variation in the amount of fruit eaten by bats, meaning other factors unaccounted for probably considerably influenced the bats' feeding behaviour. Despite the higher bat damage in early night (18:00 - 00:00) for 45%, 59% and 58% of sampling cycles (tree per night) at Calebasses, Beaux Songes and backyards respectively (up to 101 more fruits per tree per night), we also found instances of higher damage in late night (00:00 – 06:00; 34%, 26% and 20% respectively), up to 47 fruits per tree per night. The AudioMoth recorded deliberate disturbances at both orchards throughout the cycle with an average duration proportion of 3.0±1.4% and 2.7±2.3% at Beaux Songes for before and after midnight respectively and 1.6±1.1% and 1.0±1.0% at Calebasses. Five different types of disturbances were recorded and they were either noise-based deterrence (firecracker/gunshot, sound of stick hitting empty barrel, whistling and shouting) or visibility-based (burning of leaves/branches/tyres) which could also be detected with the AudioMoth by the sound of crackling and sputtering during burning. However, since we were restricted to using a single AudioMoth throughout the fruiting season, we did not have enough data for more detailed analysis about the influence of such disturbances in foraging bats.

Temporal pattern of bird foraging behaviour

In contrast to bats, we found weak to moderate evidence that birds eat a slightly larger number of fruit toward the end of the study in both orchards (Table 1, Fig. 3). However, the relatively large *SEs* indicate that more observations are needed to obtain more precise estimates. We also found strong evidence that birds eat most fruits during early and late morning in Beaux Songes (00:00 – 06:00 and 06:00 – 12:00) and in late morning and afternoon in Calebasses (06:00 – 12:00 and 12:00 – 18:00) (Table 1, Fig. 3). The $R^2_{marginal}$ indicated that our predictors explained a considerable amount of variation (65%) in the amount of fruit eaten by birds.

Fruit ripeness effect on foraging behaviour of bats and birds

We found strong evidence that bats generally eat higher proportions of lychee flesh than parakeets with varying degrees of fruit ripeness in Beaux Songes, except for fully ripe fruits (Table 2). In Beaux Songes we also found weak evidence that bats eat more flesh than birds for unripe fruits and strong evidence that parakeets generally eat less flesh than other birds for fully and partly unripe fruit (ripeness stages 0%, 25% and 50%). In Calebasses, we found no evidence that bats eat a higher proportion of flesh than parakeets or other birds, and some evidence that parakeets eat a smaller proportion of flesh than other birds for some unripe fruits (25% ripeness). Furthermore, we found strong evidence that bats eat higher proportions of flesh as fruit ripeness increases in both orchards, and moderate evidence for a similar trend for parakeets in one orchard (Beaux Songes) (Fig. 4). Finally, we also found strong evidence that bats in Beaux Songes eat higher proportions of flesh towards the end compared to the beginning of the study. However, the small number of observations for parakeets and other birds for some levels of fruit ripeness resulted in large *SE*s, meaning additional observations are required to estimate the trends for parakeets and other birds more accurately. The low $R^2_{marginal}$ indicated that other factors that we did not account for may explain a larger amount of variation in the proportion of flesh eaten by different animals. Additionally, the average weight of ripe lychee was 21.3±2.3 g (n = 42).

Discussion

Ecological implications

Our findings reiterated previous findings that flying foxes prefer ripe fruits (Luft, Curio & Tacud, 2003; Krivek et al., 2020; Reinegger et al., 2021) since they ate more fruit flesh with increasing ripeness at both orchards and more fruit flesh towards the end of the study at Beaux Songes. This trend was not apparent at Calebasses as all fruits were eaten before they ripened for most of the assessed trees. However, bat damage started with unripe fruits and most damage occurred between unripe and 25% ripened fruits where bats barely consumed fruit flesh. This behaviour is common in foraging animals as they tend to become more choosy during high fruit availability when the probability of obtaining fruits of higher quality increases (Pyke, 1984; Janson, 1996; Whitehead, Quesada & Bowers, 2016). Remarkably, ring-necked parakeets also ate larger proportions of flesh with increasing fruit ripeness in Beaux Songes, indicating that they also target ripe lychee flesh. This shows that they can be more frugivorous than granivorous (Shivambu, Shivambu & Downs, 2021). Consequently, like *P. niger*, *A. krameri* was also more wasteful when feeding on unripe fruits, similar to findings by Sebastián-González et al. (2019), although additional observations are needed to confirm how strong this trend is among parakeets in Mauritius because most fruits had been consumed when unripe leaving scanty ripe ones. For both orchards, frugivores ate less fruits towards the end of the fruiting period because fewer fruits remained on trees as they had already started depleting fruits from the beginning. Much of the variation in flying fox feeding intensity remained unexplained by foraging time or study period. However, since GLMMs residual plots indicated homoskedasticity and no other deviations, the observed effects of these predictors were still relevant. Differences between trees explained a greater proportion of variation in feeding intensity. Hence, factors such as proximity to other fruiting trees and crop size could have affected fruit choice and frugivore's foraging intensity (Manasse & Howe, 1983; Ortiz-Pulido, Albores-Barajas & Díaz, 2007). Hengjan et al. (2018) found a correlation between number of fruits dropped at different hours and frequency of flying fox visits. Hence, amount of fruit eaten by *P. niger* was considered as an indicator for its density. *Pteropus niger* demonstrate seasonal movement patterns depending on food availability (Oleksy et al., 2019) with more flying foxes foraging outside natural forest areas during commercial fruiting seasons (Seegobin, Oleksy & Florens, 2022). Studying *P. alecto*, Markus & Hall, (2004) showed its tendency to fly directly towards known foraging sites at nightfall. Another study on *Rousettus aegyptiacus* suggested that experienced bats time their visits with an understanding of tree phenology and showed that bats that have not eaten much and did not drink for 12 hours would leave their colony early to target water-rich fruits compared to late-leaving bats seeking protein-rich fruits (Harten et al., 2024). The higher bat density recorded in early night at Beaux Songes orchard and undisturbed backyards suggests that they were targeting familiar foraging patches with energy and water-rich foods.

Our study occurred in summer with sunrise around 40 minutes before 06:00 and sunset 35 minutes after 18:00, explaining the record of bird damage at "night" (approximated to 18:00-06:00 in our study). Studies that modeled the optimal foraging behaviour of birds by including predation and starvation risks often predicted a bimodal feeding pattern with early morning and late evening peaks (Bednekoff & Houston, 1994; McNamara, Houston & Lima, 1994). Since our study was limited to diurnal data collected before and after noon, we could not investigate this bimodality. However, we found an early morning foraging peak followed by a decreasing rate of foraging throughout the day at both orchards. This peak could be explained by unpredictable food sources (influenced by weather changes and interruptions by competitors and predators) and a higher starvation risk in early morning pushing the birds to replenish energy reserves exhausted overnight (Bednekoff & Houston, 1994). When feeding is uninterrupted, birds are expected to decrease their foraging activity the rest of the day, feeding to maintain energy reserves and low predation risk (Bednekoff & Houston, 1994; McNamara, Houston & Lima, 1994). At Calebasses, foraging was significantly higher roughly one hour after sunrise. At Beaux Songes, however, the foraging peaked from sunrise possibly due to the residing large colony of village weaver nesting on *Casuarina equisetifolia* trees found inside the orchard. This is an additional and fourth alien bird species feeding on lychee in Mauritius compared to Oleksy et al. (2021).

Applications

Non-netted orchard lychee trees sustained high fruit losses to bats despite being subjected to some degree of sound and smoke deterrence. These deterrence practices are common in most

Mauritian orchards. Orchard owners would either camp there during fruiting season or employ people to do so to actively deter bats and thieves at night. Despite the higher bat damage recorded before compared to after midnight at Calebasses, the difference was not statistically significant. Since both orchards were subjected to active deterrence, it appears that flying foxes at Calebasses could have been more affected as the difference in the duration of disturbance before and after midnight was higher than at Beaux Songes. Disturbances may have varied in intensity between different parts of the orchards too, further explaining between-tree differences in flying fox foraging intensity. Hence, to maximize time and resources, active deterrence could be concentrated during early nights in orchards where people are not camping all night (could protect a maximum of 42 kg more lychee per tree per night). While deliberate human disturbances involving the use of smoke or sound has been reported in Australia and India to deter frugivorous bats (Srinivasulu & Srinivasulu, 2001; Bicknell, 2002), their effectiveness in decreasing bat damage in orchards remained to be studied and no such study has been published in Mauritius yet. Thus, there is a need to focus future research on the assessment of these methods individually, consolidating the study with sufficient soundscape sampling (e.g. using many AudioMoths) to cover the entire orchard.

Oleksy et al. (2021) assessed fruit damage in 2015 at the same orchards as in our study to show the efficacy of netting trees and they recorded bat damage of 9% and 53% for non-netted lychee trees at Calebasses and Beaux Songes respectively. Furthermore, since 2009, the Mauritian Government has been providing subsidies to purchase nets for orchards and backyard gardens (Government of Mauritius, 2010). The higher bat damage recorded in our study suggests that the considerable increase in the use of nets in orchards during the last seven years may be displacing the damage by frugivores away from netted trees to concentrate them onto the fewer trees that remain unprotected. This would highlight the importance of protecting trees with methods proven as effective. Additionally, frugivore damage, especially by *P. niger*, started at week seven after fruit set (following lychee ripeness stages (Wei et al., 2013; Chang et al., 2015)). Hence, setting up these tree protection methods at latest in the sixth week after fruit set is advisable, a practice that is rare among most orchard owners who often wait for fruits to start ripening (G Bhanda, pers. obs).

Bird damage was relatively low and bird sonor deterrence (clapping, shouting and music) was occasionally used. Birds also seemed less affected by sonor deterrence, possibly explaining why a much larger amount of variation in bird foraging intensity was explained by time slot and cycle. Fruit loss by rats was negligible apparently because rodenticides are used after fruit set. Even though macaques do visit Beaux Songes orchard (GB pers. obs. 2018), their damage remained negligible. Macaques typically do not swallow lychee-sized seeds (Tsuji & Su, 2018), but may store them in their cheek pouches or carry them away in their hands over distances >20 m (Corlett & Lucas, 1990), particularly when disturbed by humans during crop raiding (from up to 200 m; RR pers. obs. 2024). Fruit loss by other factors was low because practices like watering adequately and frequently during fruiting to decrease the occurrence of fruit cracking (Marboh et al., 2017) and preventively spraying fungicides, were common. Furthermore, the maintenance of windbreaks around orchards could have reduced natural fruit fall. Apart from bat damage, damage by birds, alien mammals and other factors aligned with Oleksy et al. (2021). While this is the first study to quantify temporal variations of frugivore damage in orchards in Mauritius, further studies could investigate frugivory variation with tree crop sizes, orchard sizes and during successive seasons; bird's foraging intensity at more than two time periods during the day; and assessing alternative methods of crop raiding by macaques using camera traps paired with direct observations.

Conclusions

This study quantified fruit damage partitioning between diurnal and nocturnal species, permitting a more precise understanding of the extent of damage done by frugivores through time on a 24-hour basis and throughout the lychee season. Active deterrence methods in orchards would be optimised if concentrated in early night (18:00 – 00:00) and early in the season (six weeks after fruit set) for flying foxes, and in early morning for birds. Early tree protection by netting (before the seventh week after fruit set) between the first week of October and first week of November (taking into consideration intra and inter annual range for fruit set) can also be encouraged by ensuring an early and adequate supply of bird nets in the local market. These practices combined should equip managers with improved temporally-responsive tree protection action that would produce higher returns per unit of investment thereby contributing towards alleviating the HWC between fruit growers and fruit bats.

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Figure 1

Mauritius in the Indian Ocean and location of the study sites. Morc. stands for Morcellement

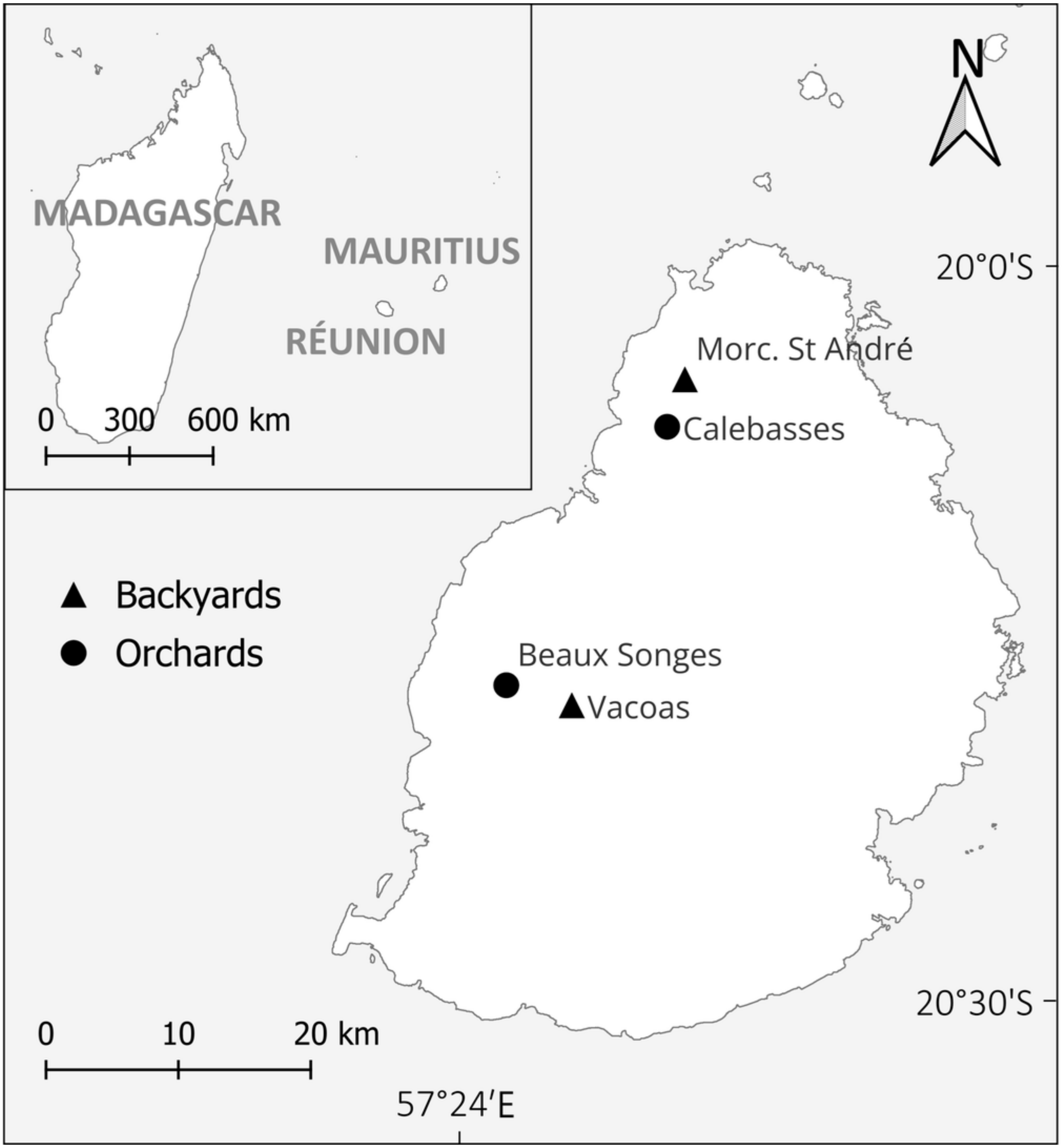


Figure 2

Bite marks on lychee eaten by different animals.

(A, B) Bats leave triangular shaped punctures on the pericarp, pulp or seed from their canines. (C) Birds (except parakeets) peck holes and feed on the pulp around the seed. (D) Parakeets tend to scrape the pulp from the top of the fruit. (E) Rats target the seed, leaving incisors marks. (F) Macaques leave incisors marks on the pericarp, pulp or seed. The scale is for images C and F only.

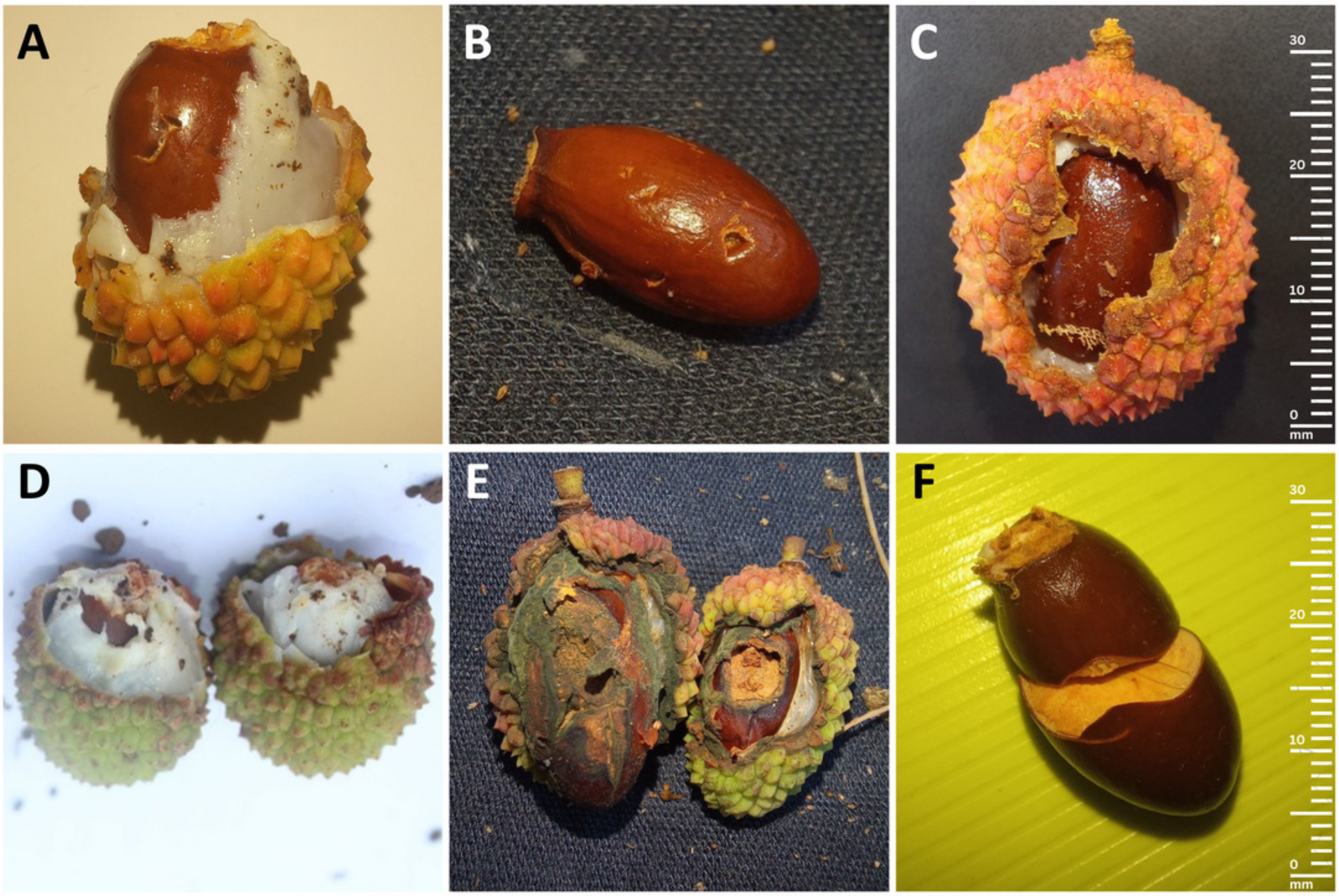


Table 1(on next page)

Effects of time slot and cycle on the number of fruits eaten by bats and birds

The Generalized Linear Mixed Models (GLMMs) explaining the effects of time slot (06:00 – 12:00, 12:00 – 18:00, 18:00 – 00:00 and 00:00 – 06:00) and cycle on the number of fruits eaten by bats and birds on lychee trees in backyards and two orchards (Beaux Songes and Calebasses). For two-way interactions between time slot and site, we provided regression coefficients, standard errors (SEs) and 95% Confidence Intervals (CIs) for the pairwise comparisons between time slots for every level of site. For two-way interactions between cycle and site, we provided regression coefficients, SEs and CIs for the slope of cycle for every level of site. Regression coefficients are provided in the following format: Coefficient ± SE (CI_{low}, CI_{up}). Effects for which the 90%, 95% or 99% CIs do not overlap zero are written in bold. The final table two rows contain marginal and conditional R^2 values of the model.

	Response variable	
Predictor/interaction	Fruits eaten by bats	Fruits eaten by birds
Backyards: time slot		
00:00 – 06:00 vs. 18:00 – 00:00	**-0.55 ± 0.21 (-0.96, -0.14)**	-
Beaux Songes: time slot		
06:00 – 12:00 vs. 12:00 – 18:00	-	**1.35 ± 0.24 (0.73, 1.98)**
06:00 – 12:00 vs. 18:00 – 00:00	-	**3.22 ± 0.45 (2.08, 4.37)**
06:00 – 12:00 vs. 00:00 – 06:00	-	0.41 ± 0.21 (-0.12, 0.94)
12:00 – 18:00 vs. 18:00 – 00:00	-	**1.87 ± 0.47 (0.67, 3.07)**
12:00 – 18:00 vs. 00:00 – 06:00	-	**-0.94 ± 0.25 (-1.58, -0.31)**
00:00 – 06:00 vs. 18:00 – 00:00	**-0.38 ± 0.12 (-0.62, -0.14)**	**2.81 ± 0.45 (1.66, 3.97)**
Calebasses: time slot		
06:00 – 12:00 vs. 12:00 – 18:00	-	**1.10 ± 0.21 (0.57, 1.63)**
06:00 – 12:00 vs. 18:00 – 00:00	-	**5.65 ± 0.74 (3.75, 7.55)**
06:00 – 12:00 vs. 00:00 – 06:00	-	**4.02 ± 0.38 (3.05, 5.00)**
12:00 – 18:00 vs. 18:00 – 00:00	-	**4.55 ± 0.74 (2.65, 6.46)**
12:00 – 18:00 vs. 00:00 – 06:00	-	**2.93 ± 0.38 (1.94, 3.91)**
00:00 – 06:00 vs. 18:00 – 00:00	-0.10 ± 0.15 (-0.39, 0.19)	1.63 ± 0.81 (-0.44, 3.69)
Cycle		
Backyards	0.04 ± 0.04 (-0.03, 0.12)	-
Beaux Songes	**-0.15 ± 0.02 (-0.18, -0.11)**	**0.05 ± 0.02 (0.00, 0.10)**
Calebasses	**-0.11 ± 0.03 (-0.17, -0.04)**	**0.09 ± 0.04 (0.02, 0.16)**
$R^2_{marginal}$	0.11	0.65
$R^2_{conditional}$	0.36	0.71

Figure 3

Fruit eaten by bats and birds at different time slots

(A) Predicted means and 95% confidence intervals for total fruits eaten by bats before (18:00 – 00:00) and after midnight (00:00 – 06:00) in the selected orchards (Beaux Songes and Calebasses) and backyards, and for total fruits eaten by birds for different time slots (06:00 -12:00, 12:00 – 18:00, 18:00 – 00:00 and 00:00 – 06:00) in the selected orchards as estimated by our Generalized Linear Mixed Models (GLMMs). (B) Lines of best fit estimated by our two Generalized Linear Mixed Models (GLMMs) expressing the relationship between cycle and fruits eaten by bats in the selected orchards (Beaux Songes and Calebasses) and backyards (top), and fruits eaten by birds in the selected orchards. One cycle is defined as a full 24-hour period.

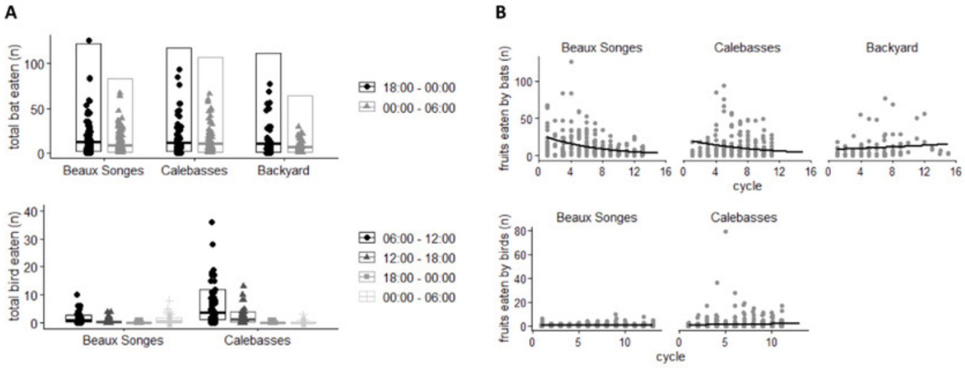

A
total bat eaten (n)
0
50
100
Beaux Songes
Calebasses
Backyard
18:00 - 00:00
00:00 - 06:00
total bird eaten (n)
0
10
20
30
40
Beaux Songes
Calebasses
06:00 - 12:00
12:00 - 18:00
18:00 - 00:00
00:00 - 06:00
B
Beaux Songes
Calebasses
Backyard
fruits eaten by bats (n)
0
50
100
0
4
8
12
16
cycle
Beaux Songes
Calebasses
fruits eaten by birds (n)
0
20
40
60
80
0
5
10
cycle

Table 2(on next page)

Effects of cycle and fruit ripeness on the proportion of lychee flesh eaten by bats and birds

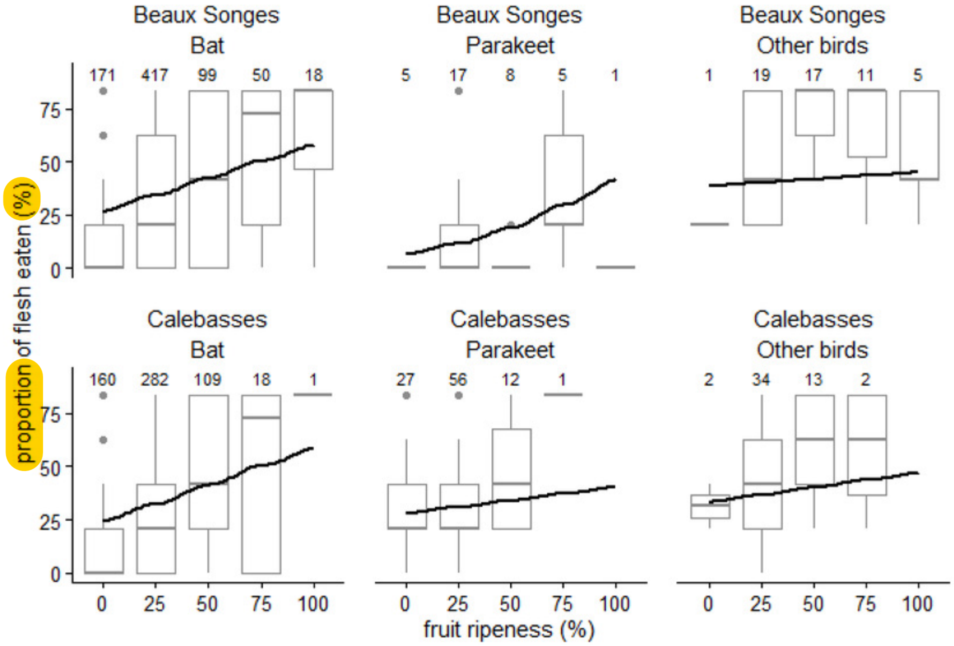
The Generalized Linear Mixed Model (GLMM) explaining the effects of cycle and fruit ripeness on the proportion of flesh eaten of lychee fruits by different animals (bats, parakeets and other birds) in our two orchard sites (Beaux Songes and Calebasses). For the three-way interaction between animal, fruit ripeness and site, we provided regression coefficients, standard errors (*SE*s) and 95% Confidence Intervals (CIs) for the pairwise comparisons between the different animals for every level of site and fruit ripeness (0%, 25%, 50%, 75% and 100%). For both three-way interactions in our model (fruit ripeness, animal and site, and cycle, animal and site), we also provided regression coefficients, *SE*s and CIs for the slope of fruit ripeness and cycle for every level of site for every animal. Regression coefficients are provided in the following format: Coefficient ± *SE* (CI_{low}, CI_{up}). Effects for which the 90%, 95% or 99% CIs do not overlap zero are written in bold. The final table two rows contain marginal and conditional R^2 values of the model.

	Sites	
Predictors/interactions	Beaux Songes	Calebasses
Animals: bats – parakeets		
ripeness 0%	**1.69 ± 0.59 (0.31, 3.06)**	-0.20 ± 0.16 (-0.57, 0.17)
ripeness 25%	**1.47 ± 0.36 (0.63, 2.32)**	0.08 ± 0.10 (-0.14, 0.30)
ripeness 50%	**1.26 ± 0.26 (0.65, 1.87)**	0.37 ± 0.19 (-0.07, 0.80)
ripeness 75%	**1.04 ± 0.39 (0.12, 1.96)**	0.65 ± 0.32 (-0.10, 1.40)
ripeness 100%	0.83 ± 0.63 (-0.64, 2.29)	0.93 ± 0.46 (-0.14, 2.00)
Animals: bats – other birds		
ripeness 0%	**-0.62 ± 0.27 (-1.24, 0.01)**	-0.50 ± 0.25 (-1.08, 0.08)
ripeness 25%	-0.30 ± 0.17 (-0.71, 0.11)	-0.23 ± 0.13 (-0.52, 0.06)
ripeness 50%	0.02 ± 0.18 (-0.41, 0.44)	0.04 ± 0.18 (-0.37, 0.46)
ripeness 75%	0.34 ± 0.28 (-0.32, 0.99)	0.32 ± 0.33 (-0.46, 1.09)
ripeness 100%	0.65 ± 0.41 (-0.30, 1.61)	0.59 ± 0.50 (-0.58, 1.76)
Animals: parakeets – other birds		
ripeness 0%	**-2.30 ± 0.62 (-3.77, -0.84)**	-0.30 ± 0.28 (-0.95, 0.35)
ripeness 25%	**-1.77 ± 0.39 (-2.68, -0.87)**	**-0.31 ± 0.14 (-0.64, 0.02)**
ripeness 50%	**-1.24 ± 0.30 (-1.94, -0.54)**	-0.33 ± 0.23 (-0.87, 0.23)
ripeness 75%	-0.71 ± 0.46 (-1.78, 0.37)	-0.33 ± 0.42 (-1.32, 0.66)
ripeness 100%	-0.17 ± 0.71 (-1.84, 1.50)	-0.34 ± 0.63 (-1.81, 1.12)
Fruit ripeness		
bats	**1.58 ± 0.22 (1.14, 2.02)**	**1.76 ± 0.25 (1.27, 2.25)**
parakeets	**2.44 ± 1.07 (0.35, 4.53)**	0.63 ± 0.53 (-0.41, 1.67)
other birds	0.31 ± 0.55 (-0.76, 1.38)	0.67 ± 0.66 (-0.62, 1.97)
Cycle		
bats	**0.03 ± 0.01 (0.01, 0.06)**	0.02 ± 0.02 (-0.02, 0.06)
parakeets	-0.01 ± 0.11 (-0.22, 0.20)	-0.01 ± 0.03 (-0.07, 0.05)
other birds	0.07 ± 0.04 (-0.02, 0.15)	0.05 ± 0.04 (-0.03, 0.14)
$R^2_{marginal}$	0.17	
$R^2_{conditional}$	0.19	

Figure 4

Amount of fruit flesh eaten by bats and birds with varying ripeness

The lines of best fit estimated by our Generalized Linear Mixed Model (GLMM) expressing the relationship between the stage of fruit ripeness and proportion of flesh eaten by bats, parakeets and other birds in two orchards (Beaux Songes and Calebasses). Boxplots of the raw data are also shown to illustrate the distribution of the data for different stages of fruit ripeness for each animal in the two orchards. Number of observations per site, animal and stage of fruit ripeness are indicated above every boxplot.


Beaux Songes
Bat
171 417 99 50 18
Beaux Songes
Parakeet
5 17 8 5 1
Beaux Songes
Other birds
1 19 17 11 5
Calebasses
Bat
160 282 109 18 1
Calebasses
Parakeet
27 56 12 1
Calebasses
Other birds
2 34 13 2
proportion of flesh eaten (%)
0
25
50
75
0
25
50
75
100
fruit ripeness (%)