Ripeness Preferences in Seba's Short Tailed-Fruit Bats, Carollia perspicillata

Authors: Christiano, Brandi, Weikel, Marina, James, Logan, Ryan, Michael, and Page, Rachel

Source: Acta Chiropterologica, 27(1) : 75-83

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/15081109ACC2025.27.1.007

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Acta-Chiropterologica on 11 Aug 2025
Terms of Use: https://bioone.org/terms-of-use Access provided by University of Texas at Austin

Acta Chiropterologica, 27(1): 75–83, 2025
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/15081109ACC2025.27.1.007

Ripeness preferences in Seba's short tailed-fruit bats, *Carollia perspicillata*

BRANDI CHRISTIANO[1, 2, 3, 4], MARINA WEIKEL[2], LOGAN JAMES[2, 3], MICHAEL RYAN[2, 3], and RACHEL PAGE[3]

[1]*Bat Conservation International, 500 N Capital of Texas Hwy Bldg. 8-225, Austin, USA*
[2]*Integrative Biology, The University of Texas at Austin, 2415 Speedway, 78712, Austin, USA*
[3]*The Smithsonian Tropical Research Institute, Apartado, 0843-03092, Balboa Ancón, Panama*
[4]*Corresponding author: E-mail: brandi.christiano24@gmail.com*

Animals use various criteria to optimize their foraging decisions. Frugivorous bats meet nearly all their nutritional needs from the fruits they consume, and various studies indicate that different fruit qualities can affect the feeding behaviour. This could reflect the evolutionary history and mutual influence of plants and frugivores. However, sugar preferences among frugivorous mammals are inconsistent. This study compares the ripeness preferences of the ecologically important fruit-eating bat, *Carollia perspicillata*, in Panama. We demonstrate that sugar content significantly predicts both the quantity and quality of consumed fruit. We find bats to exhibit strong preferences for ripe and overripe fruits, foraging on them more quickly than unripe fruits, which were consistently less favoured. We also discuss how internal factors may influence the foraging decisions of these bats.

Key words: sugar content, *Carollia perspicillata*, foraging behaviour, fruit ripeness

Los animales utilizan varios criterios para optimizar sus decisiones de búsqueda de alimento. Los murciélagos frugívoros satisfacen casi todas sus necesidades nutricionales a partir de las frutas que consumen, y varios estudios indican que las diferentes calidades de las frutas pueden afectar el comportamiento alimentario. Esto podría reflejar la historia evolutiva y la influencia mutua de plantas y frugívoros. Sin embargo, las preferencias por el azúcar entre los mamíferos frugívoros son inconsistentes. Este estudio compara las preferencias de madurez del murciélago frugívoro de importancia ecológica, *Carollia perspicillata*, en Panamá. Demostramos que el contenido de azúcar predice significativamente tanto la cantidad como la calidad de la fruta consumida. Descubrimos que los murciélagos exhiben fuertes preferencias por las frutas maduras y demasiado maduras, buscándolas más rápidamente que las frutas inmaduras, que eran consistentemente menos favorecidas. También discutimos cómo los factores internos pueden influir en las decisiones de alimentación de estos murciélagos.

Palabras clave: contenido de azúcar, *Carollia perspicillata*, comportamiento de búsqueda de alimento, madurez del fruto

INTRODUCTION

Food choice is critical for an animal's well-being; thus, animals are assumed to seek resources of the highest relative energy value (Stephens and Krebs, 1986). But species differ in the criteria they use to make foraging decisions. For example, woodland birds selectively forage on insects with greater levels of crude protein (Razeng and Watson, 2015) and rhesus macaques use texture to identify higher-quality foods (Huang *et al*., 2021). An animal's foraging choices can change with the characteristics of its surrounding environment; therefore, understanding the different factors that shape foraging decisions is important for determining the impact of a species in ecosystems.

Frugivores play an important role in shaping plant communities by consuming and dispersing seeds of fruits (Fleming, 1993; Rumeu *et al*., 2020). In tropical forests, 50–90% of shrub and tree species rely on frugivorous animals to disperse their seeds (Fleming *et al*., 1987), resulting in strong selective pressures for plants to match the preferences of the animals that consume them (Valenta and Nevo, 2022). The relationships between zoochorous fruits and their dispersers are reflected in 'seed dispersal syndromes' (Janson, 1983). These syndromes emerge through evolutionary changes in plant traits such as colour, odour, and size, which enhance fruit detection and subsequent seed removal by dispersal agents (Hodgkison *et al*., 2013; Ripperger *et al*., 2014). For instance, visually oriented frugivores favour brightly coloured fruits that contrast with the forest background (Lomascolo and Schaefer, 2010). Of these traits, fruit odour is especially important for nocturnal animals that rely less on vision to locate food. Frugivorous bats that forage at night use olfactory cues to find food in the forests (Kalko *et al*., 1996; Ripperger *et al*., 2014). Hence, mature and ripe chiropterochorous fruits tend to produce strong odours and, therefore, attract foraging bats (Rieger and Jakob, 1988). Supporting this, Mahandran *et al*. (2021) show that the concentration of volatile compounds increases as 'bat fruits' ripen, and Luft *et al*. (2003) show that bats in the family Pteropodidae can successfully assess fruit ripeness based on odour, emphasizing the importance of fruit maturity for bat foraging.

Frugivorous bats obtain nearly all their nutritional requirements from the fruits they consume (Herbst, 1986; Delorme and Thomas, 1996), but detecting fruit ripeness is a problem most nocturnal animals face (Luft *et al*., 2003). Riper fruits contain more sugar and emit stronger odours. Therefore, if animals use odour as a cue to find appropriate foods, then bats should prefer fruits with higher sugar levels. Various studies suggest that different fruit qualities influence the feeding behaviour of bats. Old World fruit bats (Pteropodidae) show preferences for fruit hardness (Dumont and O'Neal, 2004) and pulp type (Bollen and Van Elsacker, 2002), and New World fruit bats (Phyllostomidae) show preferences for certain fruit shapes (Kalko and Condon, 1998; von Helversen and von Helversen, 1999). These preferences could reflect the evolutionary history and mutual influence of plants and frugivores. However, sugar preferences, specifically in frugivorous mammals, are not consistent (Coleman and Downs, 2012).

Carollia perspicillata (Phyllostomidae) is a common bat species found throughout the Neotropics. This species primarily relies on *Piper* infructescences, which constitute nearly 65% of their diet (Salazar *et al*., 2013). Each night, the number of ripening fruits greatly decreases, leading to reduced food availability and potential exploitative competition (Bonaccorso *et al*., 2007). These factors specifically cause different bat species in India (Pteropodid) to consume unripe fruits (Sudhakaran and Doss, 2012), which are arguably less nutritionally desirable. If *C. perspicillata* faces the same constraints, perhaps they exhibit similar foraging choices. We predict that *C. perspicillata* will consume unripe fruits if that is the only option available but will prefer ripe or overripe fruits. In this study, we tested ripeness preferences of *C. perspicillata* in Panama by offering novel fruit that varied in ripeness. We measured the amount of each ripeness category that was eaten, the latency to feed on each, and the preference for one ripeness over another.

MATERIALS AND METHODS

Animals and Housing

We conducted experiments between June and August 2022 at the Smithsonian Tropical Research Institute's facilities in Gamboa, Panama. We captured a total of 26 adult C. perspicillata (13 females and 13 males) from tunnels in Soberanía National Park. We determined the sex, age, body mass ($\bar{x}$ ± SD: 18.92 ± 2.09 g), forearm length (42.93 ± 1.09 mm), body condition (initial mass (g)/forearm length (mm): 0.44 ± 0.05 g/mm) and reproductive state of each individual. Males with enlarged testicles were considered reproductively active. To determine if females were reproductively active, we palpated the abdomen to detect the presence of a fetus and checked for enlarged nipples or signs of lactation. Bats were temporarily held in a tent (173 × 86 × 77 cm) for 24 hours and provided with ad libitum access to fruit (a mix of papaya, banana, pear, and sometimes watermelon). After one night of acclimation all bats were readily feeding. We then transferred each bat to an individual testing cage (60.5 × 39.5 × 41 cm). We monitored body mass daily. Following the completion of trials, we housed bats together overnight and provided a mix of fresh fruit before releasing them at their capture location. We kept bats in captivity for five to six nights and individually marked each bat with a PIT tag (Biomark Ltd, Boise, ID, USA) for future identification and to avoid inadvertent retesting. All procedures were approved by the University of Texas Institutional Animal Care and Use Committee (AUP-2022-00121), the Smithsonian Tropical Research Institute (IACUC 2020-0113-2023-A8), and the government of Panama (MiAmbiente SE/AP-22-19).

Procedures

We used a field-accessible approach to quantify the ripeness of bananas. Using a Brix refractometer (Aichose 0–80% Brix Meter), we measured the amount of sugar (in grams) in the bananas. A degree or percentage Brix is a measurement of the amount of sugar in a liquid and is a commonly used technique for measuring sugar levels in bananas (Torija *et al*., 1998; Kyamuhangire *et al*., 2002; Akmalia *et al*., 2017; Ali *et al*., 2018). We classified banana ripeness with the following scale: unripe < 15 g sugar, ripe 15–25 g, overripe > 25 g. The categories were established through repeated measurements of °Brix of each banana that corresponded with visual indicators of maturation (following Gomes *et al*., 2013): unripe (more green than yellow peel), ripe (mostly yellow peel), and overripe (brown-spotted peel). Each night, we offered bats portions of banana in different stages of ripeness.

Experiment 1: Single Choice Tests

In Experiment 1 we asked if bats would alter their food intake based on fruit ripeness (as measured using sugar content). During a foraging session, we offered bats banana placed in the centre of their individual cage for 30 minutes. Three foraging sessions took place each night, with subsequent sessions starting two hours after the previous one (Fig. 1). For each bat, the ripeness of the fruit remained the same throughout the night. Following completion of the trials, bats were housed together overnight and offered a mix of fruit that did not contain banana. On the following night, we offered fruit from a different ripeness category. We repeated this until each bat was offered each type of banana. The order of fruit ripeness offered was randomized for each bat. We completed trials for three consecutive nights to ensure each bat was offered 'unripe', 'ripe', and 'overripe' fruit. We recorded the amount of fruit each individual consumed by calculating the difference in fruit weight before and after each foraging session. To calculate the amount of banana consumed each night, we summed the total amount eaten during each trial.

Latency to feed in single choice tests

We used an infrared (IR) light and an IR-sensitive Sony Nightshot camcorder to record each trial. We then analyzed each video to record the time it took for each individual to approach a food option. We predicted bats would approach overripe fruit faster than ripe or unripe fruit. We also predicted bats would approach ripe fruit faster than unripe fruit.

Experiment 2: Two Choice Tests

For Experiment 2, we asked if bats would discriminate among foods that varied in ripeness. On the fifth night, bats were individually offered a choice of two bananas that varied in ripeness. We presented bats with pairwise combinations of unripe, ripe, or overripe bananas (Fig. 1). We conducted three 30-minute foraging sessions throughout the night for each bat. There was a two-hour interval between each session to allow bats to digest their last meal and become hungry again. We predicted that bats, when given a choice, would consume more ripe than unripe fruit and more overripe than unripe fruit.

Statistical Analyses

After first visualizing our data, we square-root transformed the total food eaten each night, and log-transformed the body condition datasets to obtain normality. For all analyses, we used linear mixed-effects models with an individual's Bat-ID as a random effect and the amount of food eaten or feeding latency as the dependent variable. Category of ripeness was our primary independent variable, as well as interactions with sex, reproductive state, and body condition. Body mass was already incorporated into our body condition variable. Therefore, we did not include it separately in our models. We analyzed the interactions between each variable separately. To compare feeding latencies, we calculated the average time each bat took to approach the food during the ripe, unripe, and overripe conditions of the single choice tests. Analyses were conducted in R (version 4.3.1) with the packages lme4 (Bates *et al*., 2009) and lmerTest (Kuznetsova *et al*., 2015). A priori power analyses were conducted to evaluate differences between the treatment groups with a medium effect size (0.50), and an alpha of 0.05 for each group. Results showed the sample sizes of our study were enough to achieve a power of 0.80 for each comparison.

RESULTS

Experiment 1: Single Choice Tests

We first conducted a linear mixed-effects model to investigate the influence of ripeness on the amount of banana consumed by bats. Given our a priori classification of bananas into three categories of ripeness (unripe: < 15%, ripe: 15–25%, overripe: > 25%), we confirmed that ripeness category significantly predicted the amount of food

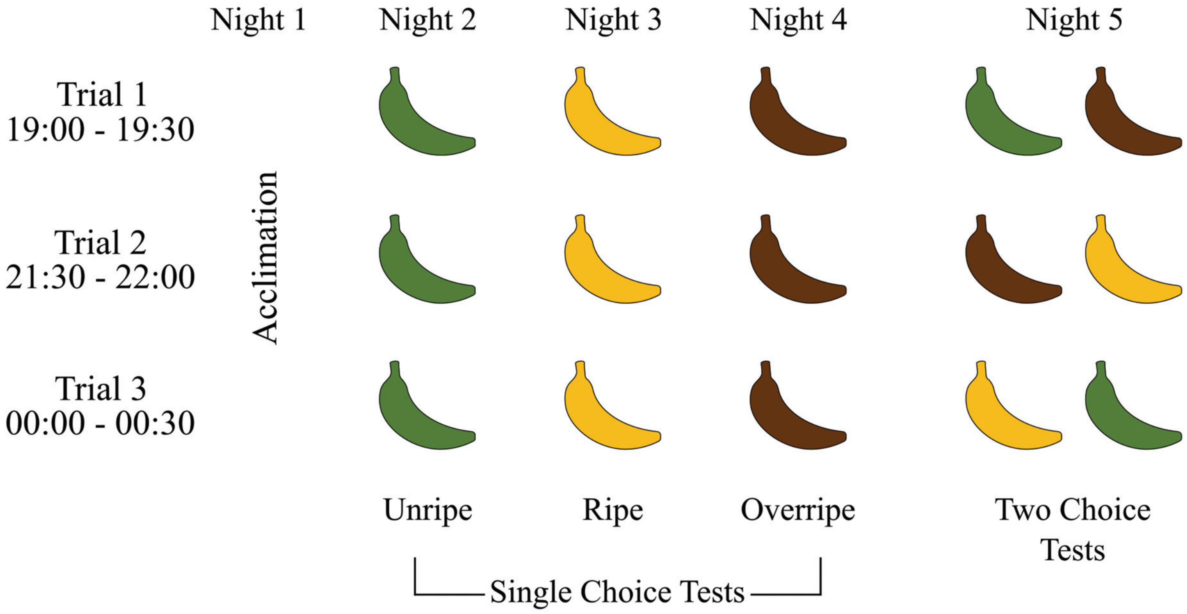

FIG. 1. An example of the experimental setup for an individual bat. In Experiment 1 (nights 2–4), bats were individually offered a single choice of bananas that varied in ripeness. In Experiment 2 (night 5), bats were offered a choice between two portions of bananas that varied in ripeness. Presentation order was randomized across bats

consumed ($F_{2,\ 56} = 24.6$, $P < 0.001$), with bats consuming less unripe banana than either ripe or overripe (unripe and ripe: $t_{59.5} = 6.9$, $P < 0.001$; unripe and overripe: $t_{56.5} = 5.4$, $P < 0.001$ — Fig. 2A). Irrespective of the sugar classification, we found a significant predictive link between sugar content (% Brix) and food consumption ($F_{1,\ 61.2} = 33.5$, $P < 0.001$).

The models suggested potential effects of sex and reproductive state on food choices. However, we must emphasize the limitation of our small samples of reproductive females (*n* = 2 of 13) and non-reproductive males (*n* = 3 of 13), which constrains our ability to disentangle the effects of sex and reproductive state. Acknowledging this important limitation, we observed apparent interactions between these variables and ripeness on the amount of banana eaten (sex: $F_{2,\ 53.4} = 4.5$, $P = 0.015$; reproductive state: $F_{2,\ 54} = 3.9$, $P = 0.026$). When analyzing consumption of each ripeness category separately, we detected a statistical effect of reproductive state ($F_{1,\ 21} = 6.9$, $P = 0.016$) but not sex ($F_{1,\ 21} = 2.0$, $P = 0.167$) on the amount of overripe fruit consumed, with no significant differences for ripe or unripe fruit (Supplementary Fig. S1A). We observed no main effect of body condition, nor an interaction with ripeness, on the amount eaten.

Latency to feed in single choice tests

Latency to feed predicted the amount of fruit consumed ($F_{1,\ 57.1} = 85.3$, $P < 0.001$), and ripeness significantly predicted the latency to feed (LMM: $F_{2,\ 57} = 9.42$, $P < 0.001$). Specifically, we found that bats took more time to feed on unripe fruits than on ripe or overripe fruits ($P < 0.001$ for both comparisons — Fig. 2B). We included body condition, reproductive state, and sex in full-factorial models with ripeness. We again found significant main effects of ripeness and reproductive state on the latency to feed (ripeness: $F_{2,\ 56} = 10.7$, $P < 0.001$; reproductive state: $F_{1,\ 56} = 4.4$, $P = 0.04$), bats fed faster on riper fruits and reproductively active bats fed faster than non-reproductive bats (Supplementary Fig. S1B). We report these results with the caveat that sample sizes of reproductive and non-reproductive individuals of each sex are small.

Experiment 2: Two Choice Tests

We presented bats with a binary choice between two fruit combinations consisting of unripe vs. ripe, unripe vs. overripe, and ripe vs. overripe options. We analysed each combination independently using linear mixed-effect models. Bats consume

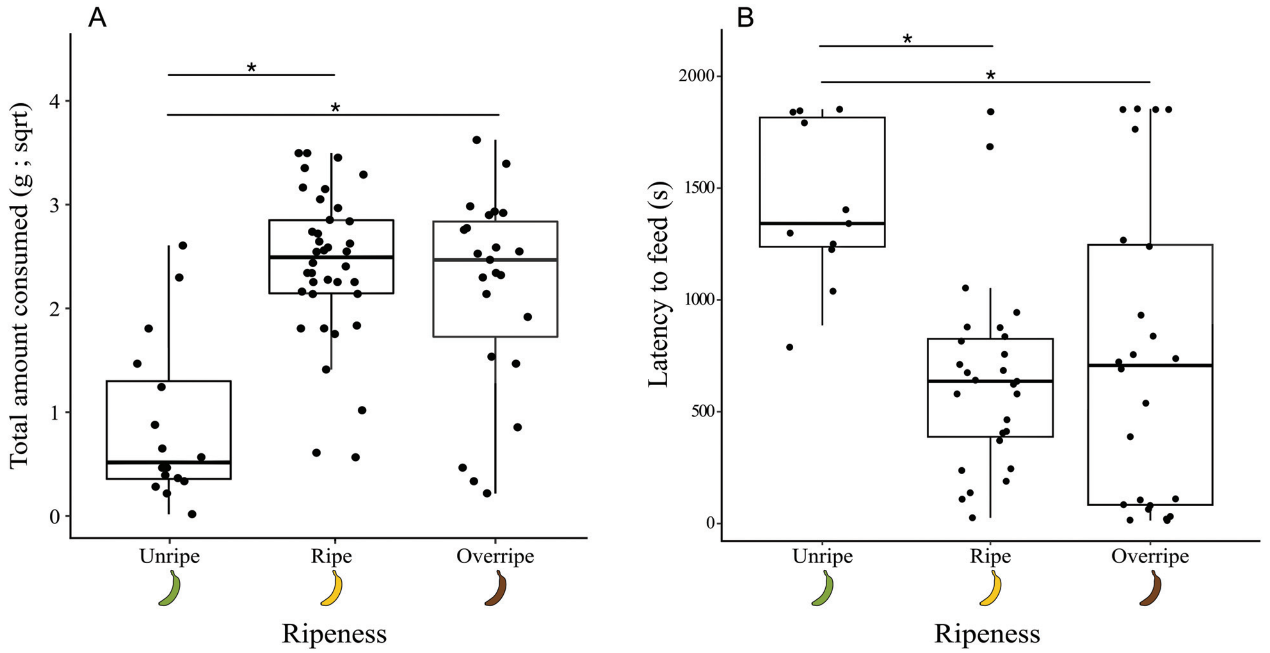

FIG. 2. The total amount of food consumed and the latency to feed in single choice tests (Experiment 1). A — The total amount of fruit in each category consumed by bats in each trial (unripe, *n* = 16; ripe, *n* = 38; overripe, *n* = 23). Bats consumed less unripe banana than ripe and overripe ($P < 0.001$ for both comparisons); B — The latency to feed on fruits in different ripeness category (unripe, *n* = 11; ripe, *n* = 26; overripe, *n* = 23). Bats took significantly longer to feed on unripe banana than on ripe and overripe ($P < 0.001$ for both comparisons). For all plots, boxplots display the medians and interquartile ranges (IQR) of the values, with the whiskers extending to the most extreme data points found within ± 1.5 times the IQR. Dots depict all individual data points

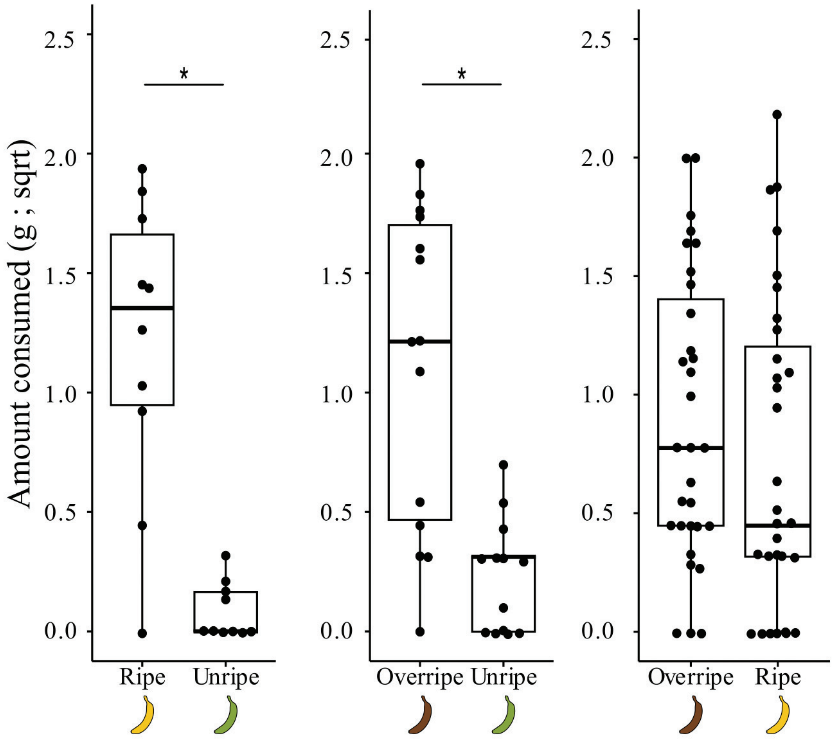

FIG. 3. The amount of fruit consumed during each of the two choice tests (Experiment 2). Bats consumed significantly more ripe banana or overripe banana compared to unripe banana (ripe, $P < 0.001$; overripe, $P < 0.001$). Boxplots display the medians and interquartile ranges (IQR) of the values, with the whiskers extending to the most extreme data points found within ± 1.5 times the IQR

significantly more ripe banana or overripe banana compared to unripe banana (ripe: $F_{1,\ 11.6} = 36.1$, $P < 0.001$; overripe: $F_{1,\ 21.1} = 22.6$, $P = 0.001$ — Fig. 3). We found no difference between the amount of ripe and overripe banana consumed during this trial ($F_{1,\ 60} = 1.0$, $P = 0.329$). Parallel to our analysis in Experiment 1, we next asked whether reproductive status, sex or body condition of bats influenced foraging decisions. We observed no significant main effects nor interaction effects for body condition and sex.

We did not observe any significant main effects or interaction effects related to reproductive status in the choice tests comparing ripe bananas with unripe or overripe bananas. However, for the choice between unripe and overripe banana, we observed a significant interaction between reproductive status and ripeness on the amount consumed ($F_{1,\ 24} = 5.8$, $P = 0.024$), with reproductively active bats consuming more overripe banana than non-reproductive bats.

DISCUSSION

Deciding which foods to eat is an important choice for all animals, especially frugivores, which have relatively selective diets to obtain their essential nutrients. For bats, specifically, there are mutual benefits for both the bat and the plant in finding ripe fruits at their peak nutrient capacity. The primary objective of this study was to explore how fruit ripeness influences the foraging decisions of Seba's short-tailed fruit bats. We revealed a significant correlation between sugar content and the amount of fruit consumed by bats. We consistently found a tendency among bats to favour ripe and overripe fruits compared to unripe fruits in all analyses involving unripe options. In the single choice tests, bats were slower to approach unripe fruit and ate less unripe fruit compared to the other categories. When given a choice between unripe and other fruit, bats consumed substantially less unripe fruit. In short, it is clear that fruit ripeness strongly influenced foraging decisions in this species. However, a limitation of our study remains in the lack of measurements of other nutrients and the investigation of only one fruit type. Given the field-based nature of our research, our focus was primarily on the sugar content of a single fruit species. We appreciate that investigating a second fruit type using similar methods would provide a stronger validation of the impact of ripeness on dietary decisions and enhance the robustness of our findings. This approach could offer a broader understanding of bat dietary choices, though it was beyond the scope of the current study. Similarly, exploration of the impact of other nutrients on bat dietary choices would further fortify the conclusions drawn. Despite these limitations, the results we present add to the growing body of literature that identifies characteristics of food that influence highly impactful species of seed dispersers in the tropics. It is not surprising that bats prefer ripe fruits, but to our knowledge this is the first study to establish their preferences and to quantify the amount and latency to consume fruits in varying stages of ripeness. From this, we discuss how important fruit ripeness, and the role of olfaction can be for nocturnal animals, especially those that are reproductively active.

Many mammalian species rely on their ability to smell. In an environment characterized by limited nutrients and an abundance of toxic plants, animals have evolved sensory systems to identify and prioritize vital nutrients. They are attracted to energy-rich plants with a sweet taste, while simultaneously avoiding bitter ones (Mennella *et al*., 2016). For frugivorous animals, particularly bats that are active at night with little access to visual cues, olfaction plays a major role in foraging (Rieger and Jakob, 1988; Parolin *et al*., 2015; Page and ter Hofstede, 2021). As fruits ripen, they release aromatic compounds, making them easier to detect. Our study results strongly support the evolution of this relationship between fruits and their dispersers. Tested bats were more attracted to and consumed more of the fruit that was in the later stages of ripeness. An excellent addition to the current study would be to examine the aromatics of the fruits and classify different compounds being released that make riper fruits more attractive.

When fruit becomes overripe, it begins to ferment and produce different alcohols (Mazeh *et al*., 2008). Ripe fruits can contain quantities of ethanol up to ~5% (Orbach *et al*., 2010). Therefore, ethanol consumption occurs in a variety of taxa, including insects, birds, and mammals (Dudley, 2000). The Drunken Monkey Hypothesis, which aims to explain the evolutionary underpinnings of human attraction to alcohol, highlights that fruit-eating animals rely on the smell of alcohol as a long-distance indicator of sugar availability, often through ripe and overripe fruits (Dudley, 2014). However, studies on birds and bats show the contrary: some birds have no preference for fruits with higher ethanol content (Zungu and Downs, 2017), and higher concentration of ethanol deterred fruit consumption in some fruit-eating bats (Korine *et al*., 2011). Although we did not measure ethanol content of the fruit in the current study, we did find that bats prefer overripe fruits, but only when compared to unripe fruits. When compared to ripe fruits, bats do not show a preference for overripe fruits, suggesting that an increase in sugar and the potential presence of ethanol are evaluated relative to the other available food options.

In many animals, behaviour can vary with reproductive state. Reproductively active animals often exhibit greater increases in energetic needs and alter their behaviours to meet those demands. For instance, female hoary bats forage longer when in later reproductive stages (Barclay, 1989). Males exhibit similar responses while facing behavioural and physiological challenges such as increased muscle mass, hormonal fluctuations (Ellison, 2003), heightened aggression (Grant and Foam, 2002), and prolonged competition (Higham *et al*., 2011). Although these studies demonstrate that reproductively active animals forage longer to match their caloric needs, less is known about how reproductive state influences an individual's decision on which foods to consume. This study did not find evidence of all bats favouring overripe fruit but suggests that reproductively active bats may favour overripe fruits. During the two-choice trials, reproductively active bats consumed more overripe fruit than non-reproductive bats when given the choice of overripe and unripe fruit. However, we must emphasize that our conclusions remain tentative due to the small sample sizes of reproductive females and non-reproductive males in our study. This sampling limitation prevents us from making definitive claims about sex-based differences or conclusively attributing the observed patterns solely to reproductive state. While our preliminary findings suggest that reproductive state might be an important factor affecting both the quantity and speed at which bats consumed fruits at various stages of ripeness, these results should be interpreted with caution and certainly merit future investigations with larger, more balanced sample sizes.

The physiological and energetic changes animals experience during times of reproduction alters how they perceive and interpret sensory information. For instance, female túngara frogs exhibit heightened visual sensitivity when reproductively active (Cummings *et al*., 2008), and this is accomplished through the direct action of estradiol on the retina (Leslie *et al*., 2021. In other examples, female midshipman fish demonstrate adaptive auditory plasticity during the breeding season (Sisneros and Bass, 2003), and African cichlid fish, both males and females, undergo shifts in their visual, olfactory, and auditory processing when breeding (Maruska and Butler, 2021). In various mammals, changes in mRNA expression occur in brain regions responsible for olfactory recognition during reproductive periods (Kendrick *et al*., 1997). These shifts can lead to increased sensitivity to certain stimuli and reduced sensitivity to others (Maruska and Butler, 2021). It is worth noting, however, that the widely held belief that olfactory sensitivity is enhanced in pregnant women appears not to be true (Cameron, 2014). Furthermore, some animals may adapt their sensory perception to locate the resources essential for reproduction better, such as suitable nesting sites (Chaib *et al*., 2023) or specific food types (Rushmore *et al*., 2012). Over the course of evolution, animals have acquired sensory adaptations that enable them to respond successfully to the particular challenges they face during the reproductive phases of their lives (Clemens *et al*., 2014; Maruska and Butler, 2021; Taub *et al*., 2023). Alternatively, animals may exhibit different behaviours based on how they process information. It would be intriguing to measure sensitivity to olfactory cues as a function of reproductive state to determine whether these preferences are due to inherent sensitivity or a higher-level decision-making process.

In conclusion, fruit-eating bats are recognized as one of the most important groups of frugivorous vertebrates in the Neotropics (de Oliveria *et al*., 2020). They play crucial ecological roles as seed dispersers (Ghanem and Voigt, 2012), and among them, phyllostomid fruit bats stand out by promoting rapid reforestation through the dispersal of seeds from early successional plants like *Cecropia, Ficus*, and *Vismia* (Ghanem and Voigt, 2012). A bat's ability to fly long distances during foraging ensures seeds are dispersed far from the parent plant, promoting plant growth in new areas (Abedi-Lartey *et al*., 2016). Understanding the internal and external factors that influence bat foraging decisions is essential for preserving their role in reforestation and maintaining Neotropical biodiversity. Moreover, continually questioning animal foraging decisions provides invaluable information about how species function in their ecosystem. These decisions can be influenced by past experiences, food availability, competition, predation risks, and hunger state. Ongoing studies aimed at uncovering additional facets of this behaviour contribute to advancing the field of behavioural ecology.

SUPPLEMENTARY INFORMATION

Contents: Supplementary Fig. S1. The total amount of food consumed and the latency to feed in single choice tests (Experiment 1) by sex. (A) The latency to feed on overripe fruit by reproductive (♂♂: *n* = 10; ♀♀: *n* = 2) and nonreproductive (♂♂: *n* = 3; ♀♀: *n* = 11) individuals. Reproductive bats forage faster than nonreproductive bats (*P* = 0.015). (B) The total amount of overripe fruit consumed by reproductive (♂♂: *n* = 10; ♀♀: *n* = 2) and nonreproductive (♂♂: *n* = 3; ♀♀: *n* = 11) bats. Reproductive state influences the amount of overripe banana consumed (*P* = 0.016). For all plots, boxplots display the medians and interquartile ranges (IQR) of the values, with the whiskers extending to the most extreme data points found within ± 1.5 times the IQR. Dots depict all individual data points. Supplementary Information is available exclusively on BioOne.

ACKNOWLEDGEMENTS

We thank the Integrative Biology Department of the University of Texas for funding this project. We thank Lauren Jones for scoring behaviour videos. We thank Gregg Cohen and the Smithsonian Tropical Research Institute for providing logistical support.

AUTHOR CONTRIBUTION STATEMENT

BC: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article; MW: research concept and design, collection and/or assembly of data, and final approval of the article; LJ: data analysis and interpretation, writing, critical revision, and final approval of the article; MR: research concept and design, critical revision, and final approval of the article; RP: research concept and design, critical revision, and final approval of the article.

LITERATURE CITED

Abedi-Lartey, M., D. Dechmann, M. Wikelski, A. Scharf, and J. Fahr. 2016. Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. Global Ecology and Conservation, 7: 12–24. doi: 10.1016/j.gecco.2016.03.005.

Akmalia, D., A. Saputro, and W. Handayani. 2017. A non-destruction measurement system based on hyperspectral imaging for sugar content in banana (*Musa* sp.). 2017 International Seminar on Sensors, Instrumentation, Measurement and Metrology (ISSIMM), 91–94.

Ali, M., R. Janius, N. Nawi, and N. Hashim. 2018. Prediction of total soluble solids and pH in banana using near infrared spectroscopy. Journal of Engineering Science and Technology, 13: 254–264.

Barclay, R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behavioral Ecology and Sociobiology, 24: 31–37.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, *et al*. 2009. Package 'lme4'. http://lme4.r-forge.r-project.org.

Bollen, A., and L. Van Elsacker. 2002. Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. Acta Chiropterologica, 4: 33–47.

Bonaccorso, F., J. Winkelmann, D. Shin, C. Agrawal, N. Aslami, C. Bonney, A. Hsu, P. Jekielek, A. Knox, S. Kopach, *et al*. 2007. Evidence for exploitative competition: comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). Biotropica, 39: 249–256.

CAMERON, E. 2014. Pregnancy and olfaction: a review. Frontiers in Psychology, 5: 72657.

CHAIB, S., O. LIND, and A. KELBER. 2023 Fast visual adaptation to dim light in a cavity-nesting bird. Proceedings of the Royal Society, 290B: 20230596. doi: 10.1098/rspb.2023.0596.

CLEMENS, J., S. KRÄMER, and B. RONACHER. 2014. Asymmetrical integration of sensory information during mating decisions in grasshoppers. Proceedings of the National Academy of Sciences of the USA, 111: 16562–16567. doi: 10.1073/pnas.1412741111.

COLEMAN, J., and C. DOWNS. 2012. The sweet side of life: Nectar sugar type and concentration preference in Wahlberg's epauletted fruit bat. Comparative Biochemistry and Physiology, 162A: 431–436.

CUMMINGS, M., X. BERNAL, R. REYNAGA, A. RAND, and M. RYAN. 2008. Visual sensitivity to a conspicuous male cue varies by reproductive state in *Physalaemus pustulosus* females. Journal of Experimental Biology, 211: 1203–1210. doi: 10.1242/jeb.012963.

DE OLIVEIRA, A., A. PULCHÉRIO-LEITE, J. RIBEIRO, and V. FERNANDES. 2020. Can *Carollia perspicillata* (Chiroptera: Phyllostomidae) induce seed germination of *Cecropia pachystachya*? Mastozoología Neotropical, 27: 194–199. doi: 10.31687/saremMN.20.27.1.0.04.

DELORME, M., and D. THOMAS. 1996. Nitrogen and energy requirements of the short-tailed fruit bat (*Carollia perspicillata*): fruit bats are not nitrogen constrained. Journal of Comparative Physiology, 166B: 427–434.

DUDLEY, R. 2000. Evolutionary origins of human alcoholism in primate frugivory. The Quarterly Review of Biology, 75: 3–15.

DUDLEY, R. 2014. The drunken monkey: why we drink and abuse alcohol. University of California Press, 184 pp.

DUMONT, E., and R. O'NEAL. 2004. Food hardness and feeding behavior in Old World fruit bats (Pteropodidae). Journal of Mammalogy, 85: 8–14.

ELLISON, P. 2003. Energetics and reproductive effort. American Journal of Human Biology, 15: 342–351. doi: 10.1002/ajhb.10152.

FLEMING, T. 1993. Plant-visiting bats. American Scientist, 8: 460–467.

FLEMING, T., R. BREITWISCH, and G. WHITESIDES. 1987. Patterns of tropical vertebrate frugivore diversity. Annual Review of Ecology and Systematics, 18: 91–109.

GHANEM, S., and C. VOIGT. 2012. Increasing awareness of ecosystem services provided by bats. Pp. 279–302 *in* Advances in the Study of Behavior (H. J. BROCKMANN, T. J. ROPER, M. NAGUIB, J. C. MITANI, and L. W. SIMMONS, eds.). Academic Press, 44: 321 pp. doi: 10.1016/B978-0-12-394288-3.00007-1.

GOMES, J., R. VIEIRA, and F. LETA. 2013. Colorimetric indicator for classification of bananas during ripening. Scientia Horticulturae, 150: 201–205.

GRANT, J., and P. FOAM. 2002. Effect of operational sex ratio on female versus male competitive aggression. Canadian Journal of Zoology, 80: 2242–2246. doi: 10.1139/z02-217.

HERBST, L. 1986. The role of nitrogen from fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. Biotropica, 39–44.

HIGHAM, J., M. HEISTERMANN, and D. MAESTRIPIERI. 2011. The energetics of male–male endurance rivalry in free-ranging rhesus macaques, *Macaca mulatta*. Animal Behaviour, 81: 1001–1007. doi: 10.1016/j.anbehav.2011.02.001.

HODGKISON, R., M. AYASSE, C. HÄBERLEIN, S. SCHULZ, A. ZUBAID, W. MUSTAPHA, T. KUNZ, and E. KALKO. 2013. Fruit bats and bat fruits: the evolution of fruit scent in relation to the foraging behaviour of bats in the New and Old World tropics. Functional Ecology, 27: 1075–1084.

HUANG, F., M. SUTCLIFFE, and F. GRABENHORST. 2021. Preferences for nutrients and sensory food qualities identify biological sources of economic values in monkeys. Proceedings of the National Academy of Sciences, 118: e2101954118. doi: 10.1073/pnas.2101954118.

JANSON, C. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. Science, 219: 187–188.

KALKO, E. K. V., and M. CONDON. 1998. Echolocation, olfaction and fruit display: how bats find fruit of flagellichorous cucurbits. Functional Ecology, 12: 364–372.

KALKO, E. K. V., E. HERRE, and C. HANDLEY. 1996. Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. Journal of Biogeography, 23: 565–576. doi: 10.1111/j.1365-2699.1996.tb00018.x.

KENDRICK, K., A. DA COSTA, K. BROAD, S. OHKURA, R. GUEVARA, F. LÉVY, and E. KEVERNE. 1997. Neural control of maternal behaviour and olfactory recognition of offspring. Brain Research Bulletin, 44: 383–395.

KORINE, C., F. SÁNCHEZ, and B. PINSHOW. 2011. Effects of ethanol on food consumption and skin temperature in the Egyptian fruit bat (*Rousettus aegyptiacus*). Integrative and Comparative Biology, 51: 432–440.

KUZNETSOVA, A., R. CHRISTENSEN, C. BAVAY, and P. BROCKHOFF. 2015. Automated mixed ANOVA modeling of sensory and consumer data. Food Quality and Preference, 40: 31–38. doi: 10.1016/j.foodqual.2014.08.004.

KYAMUHANGIRE, W., H. MYHRE, H. SØRENSEN, and R. PEHRSON. 2002. Yield, characteristics and composition of banana juice extracted by the enzymatic and mechanical methods. Journal of the Science of Food and Agriculture, 82: 478–482.

LESLIE, C. E., W. WALKOWSKI, R. ROSENCRANS, W. GORDON, N. BAZAN, M. RYAN, and H. FARRIS. 2021. Estrogenic modulation of retinal sensitivity in reproductive female túngara frogs. Integrative and Comparative Biology, 61: 231–239.

LOMASCOLO, S., and H. SCHAEFER. 2010. Signal convergence in fruits: a result of selection by frugivores? Journal of Evolutionary Biology, 23: 614–624.

LUFT, S., E. CURIO, and B. TACUD. 2003. The use of olfaction in the foraging behaviour of the golden-mantled flying fox, *Pteropus pumilus*, and the greater musky fruit bat, *Ptenochirus jagori* (Megachiroptera: Pteropodidae). Naturwissenschaften, 90: 84–87.

MAHANDRAN, V., C. MURUGAN, P. ANISHA, G. WANG, J. CHEN, and P. NATHAN. 2021. Chemical components change along the ontogeny of a bat fruit (*Neolamarckia cadamba*) with ripening asynchrony in favour of its fruit selection and seed dispersal. The Science of Nature, 108: 1–13.

MARUSKA, K., and J. BUTLER. 2021. Reproductive and social-state plasticity of multiple sensory systems in a cichlid fish. Integrative and Comparative Biology, 61: 249–268. doi: 10.1093/icb/icab062.

MAZEH, S., C. KORINE, B. PINSHOW, and R. DUDLEY. 2008. The influence of ethanol on feeding in the frugivorous yellow-vented bulbul *(Pycnonotus xanthopygos*). Behavioural Processes, 77: 369–375.

MENNELLA, J., N. BOBOWSKI, and D. REED. 2016. The development of sweet taste: From biology to hedonics. Reviews in Endocrine and Metabolic Disorders, 17: 171–178. doi: 10.1007/s11154-016-9360-5.

ORBACH, D., N. VESELKA, Y. DZAL, L. LAZURE, and M. FENTON. 2010. Drinking and flying: does alcohol consumption affect the flight and echolocation performance of phyllostomid bats? PLoS One, 5: e8993.

PAGE, R. and H. TER HOFSTEDE. 2021. Sensory and cognitive ecology of bats. Annual Review of Ecology, Evolution, and

Systematics. 52: 541–562. doi: 10.1146/annurev-ecolsys-012921-052635.

Parolin, L., S. Mikich, and G. Bianconi. 2015. Olfaction in the fruit-eating bats *Artibeus lituratus* and *Carollia perspicillata*: an experimental analysis. Anais da Academia Brasileira de Ciências, 87: 2047–2053. doi: 10.1590/0001-3765201520140519.

Razeng, E., and D. Watson. 2015. Nutritional composition of the preferred prey of insectivorous birds: popularity reflects quality. Journal of Avian Biology, 46: 89–96.

Rieger, J., and E. Jakob. 1988. The use of olfaction in food location by frugivorous bats. Biotropica, 20: 161–164.

Ripperger, S., E. Heymann, M. Tschapka, and E. Kalko. 2014. Fruit characteristics associated with fruit preferences in frugivorous bats and saddle-back tamarins in Perú. Ecotropica, 20: 53–63.

Rushmore, J., S. Leonhardt, and C. Drea. 2012. Sight or scent: lemur sensory reliance in detecting food quality varies with feeding ecology. PLoS One 7: e41558. doi: 10.1371/journal.pone.0041558.

Salazar, D., D. Kelm, and R. Marquis. 2013. Directed seed dispersal of *Piper* by *Carollia perspicillata* and its effect on understory plant diversity and folivory. Ecology, 94: 2444–2453. doi: 10.1890/12-1172.1.

Sisneros, J., and A. Bass. 2003. Seasonal plasticity of peripheral auditory frequency sensitivity. Journal of Neuroscience, 23: 1049-1058. doi: 10.1523/JNEUROSCI.23-03-01049.2003.

Stephens, D., and J. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, NJ, 247 pp.

Sudhakaran, M., and P. Doss. 2012. Food and foraging preferences of three pteropodid bats in southern India. Journal of Threatened Taxa, 4: 2295–2303.

Taub, M., O. Mazar, and Y. Yovel. 2023. Pregnancy-related sensory deficits might impair foraging in echolocating bats. BMC Biology, 21: 60. doi: 10.1186/s12915-023-01557-7.

Torija, E., C. Díez, C. Matallana, M. Camara, E. Camacho, and P. Mazarío. 1998. Influence of freezing process on free sugars content of papaya and banana fruits. Journal of the Science of Food and Agriculture, 76: 315–319.

Valenta, K., and O. Nevo. 2022. The illusiveness of seed dispersal syndromes. A commentary on: Fleshy fruit traits and seed dispersers: which traits define syndromes? Annals of Botany, 129: vi–vii.

von Helversen, D., and O. von Helversen. 1999. Acoustic guide in bat-pollinated flower. Nature, 398: 759–760.

Zungu, M., and C. Downs. 2017. Effects of ethanol on fruit selection by frugivorous birds. African Zoology, 52: 69–72.

Received 24 July 2024, accepted 25 May 2025

Associate Editor: Wiesław Bogdanowicz