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RESEARCH ARTICLE

Landing manoeuvres predict roost-site preferences in bats

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ABSTRACT

Roosts are vital for the survival of many species, and how individuals choose one site over another is affected by various factors. In bats, for example, species may use stiff roosts such as caves or compliant ones such as leaves; each type requires not only specific morphological adaptations but also different landing manoeuvres. Selecting a suitable roost within those broad categories may increase landing performance, reducing accidents and decreasing exposure time to predators. We addressed whether bats select specific roost sites based on the availability of a suitable landing surface, which could increase landing performance. Our study focused on Spix's disc-winged bats (*Thyroptera tricolor*), a species known to roost within developing tubular leaves. As previous studies show that this species relies on the leaves' apex for safe landing and rapid post-landing settlement, we predicted that bats would prefer to roost in tubular structures with a longer apex and that landing would be consistently more effective on those leaves. Field observations showed that *T. tricolor* predominantly used two species for roosting, *Heliconia imbricata* and *Calathea lutea*, but they preferred roosting in the former. The main difference between these two plant species was the length of the leaf's apex (longer in *H. imbricata*). Experiments in a flight cage also showed that bats used more consistent approach and landing tactics when accessing leaves with a longer apex. Our results suggest that landing mechanics may strongly influence resource selection, especially when complex manoeuvres are needed to acquire those resources.

KEY WORDS: *Thyroptera tricolor*, Leaf shape, Resource specialization, Biomechanics, Flight, Roosting

INTRODUCTION

The relationship between living beings and the resources they require for survival and reproduction represents one of the core topics in ecology. The most critical resources needed by animals to secure their survival include food and refuge (Pyke, 1984; Rapport, 1971), and the decision to select one resource over another is strongly influenced by various ecological, behavioural and morphological constraints (Brost et al., 2015; Machado, 2020; Shakeri et al., 2021). For example, individuals can only consume a specific food item if it is found within their home range, if competition for this resource is relatively low, when resource production or availability matches the individual's daily activity periods, and if they have the appropriate morphological structures to obtain and process this food item efficiently. Knowing the interactions among these constraints allows us to understand why major resource categories are selected (e.g. nectar versus fruits) and how animals select species within those categories or individuals within species. The latter is of particular interest because it provides the basis for natural selection in both antagonistic and mutualistic interactions (Andreazzi et al., 2017; Law, 1985; Nuismer et al., 2013; Thompson, 1988).

While many studies to date that tackle resource use have focused on the relationship between animals and their food sources (e.g. Costantini, 2014; Kamil et al., 1987; Stephens, 2008), roosts are also a key component of many species' natural history, and especially that of bats. Roosts provide sites for bats to escape predation and inclement weather conditions and to conduct crucial fitness-related activities such as copulation and lactation (Kunz, 1982). The selection of roosts is known to be influenced by various factors, including temperature, humidity, access to feeding sites, or increased protection against predators (Barros et al., 2020; Boonman, 2000; Delancey and Islam, 2020; Kerth et al., 2001; Rogers et al., 2006). However, other aspects of a species' biology can limit the range of roosting resources that can be exploited, including biomechanics. In bats, for example, landing mechanics are tightly linked to using different categories of roosting resources (Boerma et al., 2019; Riskin et al., 2009). Species that roost in stiff, horizontal roosts, including caves and cavities, typically use rotationally complex and low-impact two-point landings, while species that roost in compliant structures, such as foliage, use rotationally simple and high-impact four-point landings (Boerma, 2019). Biomechanics might also influence the selection of specific roost types within these broad-scale categories (e.g. stiff versus compliant roosts) as the way organisms move strongly determines which resources they can safely and efficiently exploit. For example, some species have long, narrow wings ideal for fast flight above the forest canopy but inadequate for manoeuvring within the dense understorey (Norberg and Rayner, 1987). These species might be prone to collision accidents if they cannot sufficiently decrease their speed as they approach roosts (Wheatley et al., 2021); or they could take longer to enter roosts, given their poor manoeuvrability, which increases energetic costs and exposure to predators (Norberg, 1996; Speakman et al., 1994). In fact, studies that have gauged tree-cavity selection in birds and bats often use accessibility arguments to explain roost-site preferences; essentially, cavities that provide easy access reduce flight costs and the risk of predation (Fisher et al., 2004; Vonhof and Barclay, 1996). However, no studies have to date quantified the association between accessibility and roost-site selection, as predicted by biomechanical constraints associated with flight.

An interesting case of extreme specialization for a specific roost type occurs in Spix's disc-winged bats, *Thyroptera tricolor* Spix

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Received 17 March 2022; Accepted 12 October 2022

1823. This species shelters inside the developing tubular leaves of plants in the order Zingiberales (Findley and Wilson, 1974; Vonhof and Fenton, 2004). To attach themselves to the smooth inner surfaces of the tubular structure, they have discs on their hands and ankles that provide adhesion primarily through suction (Riskin and Fenton, 2001; Schliemann, 1970; Wimsatt and Villar, 1966). These bats strongly depend on this type of roost because their reduced thumbs preclude them from effectively clinging to rough surfaces, as most bat species do (Riskin and Fenton, 2001). After the experimental removal of potential roost sites, they appear incapable of using alternative roosting structures (Chaverri and Kunz, 2011). A recent study by Boerma et al. (2019) also shows strong biomechanical specializations for using these furled leaf roosts. Specifically, they show that the force with which bats land on the leaves is significant (6.98 bodyweight, the highest ever recorded for bats; Boerma, 2019) and that the discs are vital for effective attachment to the leaf. Their results also suggest that the leaf's apex provides a site for safe landing and rapid post-landing settlement, a structure that is not always present in all plant species used for roosting.

This study aimed to determine whether biomechanical constraints influence roost-site selection in *T. tricolor*. Previous studies suggest that this bat prefers certain plant species and leaf shapes for roosting (Chaverri and Kunz, 2011). These preferences may relate to differences in microclimatic conditions within the leaves and to reducing conspicuousness and predation risk (Pérez-Cárdenas et al., 2019; Solano-Quesada and Sandoval, 2010). However, given the results of Boerma et al. (2019), we expect that biomechanical constraints could also be highly relevant during roost-site selection. Our study provides a thorough understanding of leaf-shape preference in natural populations, based on field observations of roost occupation, coupled with various semi-captive experiments that measure how the presence of a conspicuous apex affects landing tactics and performance. Overall, we predict that (i) bats will show a significant preference for plants with an acuminate apex over truncate leaves (short apex), given the role of this structure during landing (Boerma et al., 2019); and that (ii) landing will be consistently more effective in leaves with an acuminate apex, according to the landing patterns recorded by Boerma et al. (2019). Our experimental results strongly support that biomechanical constraints play an essential role during roost-site selection in bats.

MATERIALS AND METHODS

Ethical approval

For the handling of animals, we followed the ABS (Animal Behavior Society)/ASAB (Association for the Study of Animal Behaviour) 'Guidelines for the treatment of animals in behavioural research and teaching'. This study was conducted in accordance with the ethical standards for animal welfare of the Costa Rican Ministry of Environment and Energy, Sistema Nacional de Áreas de Conservación, permit no. SINAC-ACOPAC-RES-INV-008-2017. Protocols were also approved by the University of Costa Rica's Institutional Animal Care and Use Committee (CICUA-42-2018).

Plant species preferences

We performed systematic surveys of furled leaves at 6 study sites (Bolivar, Esquinas, Finca, Lecheria, Naranjal, Ureña) in lowland tropical forests in southwestern Costa Rica. We searched for leaves that could be used as potential roost sites by *T. tricolor*, an average of twice a month from October 2006 to July 2007. During the first 15 surveys, we quantified the number of furled leaves (i.e. potential roosts) per site by counting the number of unoccupied and occupied (i.e. roosts) leaves. Unoccupied furled leaves were only counted if their opening diameter ranged from 4 to 20 cm, following Vonhof and Fenton's (2004) results. However, occupied leaves were counted even if their opening diameter was not within that range.

We used 104 sampling events from our 6 study sites. The number of available potential roosting leaves was compared against the number of roosts (used leaves) for the two most commonly used plant species at our study sites: *Heliconia imbricata* and *Calathea lutea*. Bayesian generalized linear models were used to evaluate which parameters explain roosting leaf occupancy better (proportion of available furled leaves used as roosting sites). The number of used roosts and total available tubular leaves by plant species was used as a combined response variable modelled with a binomial distribution. We evaluated three models: one that included species and density as predictors, another that only included species, and the last that only included density. All models included the site as a random effect.

Leaf-shape preferences

To characterize leaf shape, we measured leaf height, leaf length, tip length, tip circumference and mid-circumference for undamaged roosts after capturing bats (Fig. 1A). Based on these measures, we also calculated available space (leaf length minus tip length), the ratio of tip length to tip circumference (tip length divided by tip circumference), and roost height (leaf length plus leaf height). However, available space and mid-circumference were excluded from the species classification analyses because of high collinearity. Supervised Random Forest (Breiman, 2001) was used for discriminating species based on the remaining five leaf-shape parameters (Fig. 1; see 'Statistical analyses specifications' below for further details). A randomization test on variable importance was used to identify those parameters significantly contributing to model discrimination.

Flight manoeuvres while entering leaves

We experimentally evaluated variation within flight manoeuvres employed for entering furled leaves of variable tip or apex shapes. Two types of apex shapes were used, representing the two extremes observed in the leaves used as roosts by *T. tricolor*: a pointy tip (i.e. acuminate apex) extended above the opening of the leaf (~5 cm tip length); and a leaf completely truncated above the opening of the leaf (i.e. no extended leaf area after the opening; 0 cm tip length). Single individuals were released inside a flight cage containing a plastic furled leaf of one of the two types (acuminate or truncate). Flights were videotaped using two digital cameras (SONY HDR-XR160). The order in which the leaf types were presented to bats was randomized each day. For example, on the first day, bats were presented first with an acuminate leaf and, upon successful completion of the task for ca. 5 individuals, a similar number of bats were tested the same day with a truncate leaf. The same process was reversed the next day: first, we performed the set of trials with a truncate leaf and then we switched to an acuminate leaf. The number of individuals tested per leaf type was 24 for acuminate and 14 for truncate leaves. Also, before starting, we decided to exclude juveniles and pregnant or lactating females from our experiments, as juveniles are not adept at manoeuvring during roost entrance and experience many failed attempts (personal observation). Moreover, the experiments could expose females in energetically constrained periods to unnecessary stress.

To build the flight trajectories in the tri-dimensional space, we set both cameras parallel to the ground, with their filming lines converging in the roost (Fig. S1). The frames they recorded,

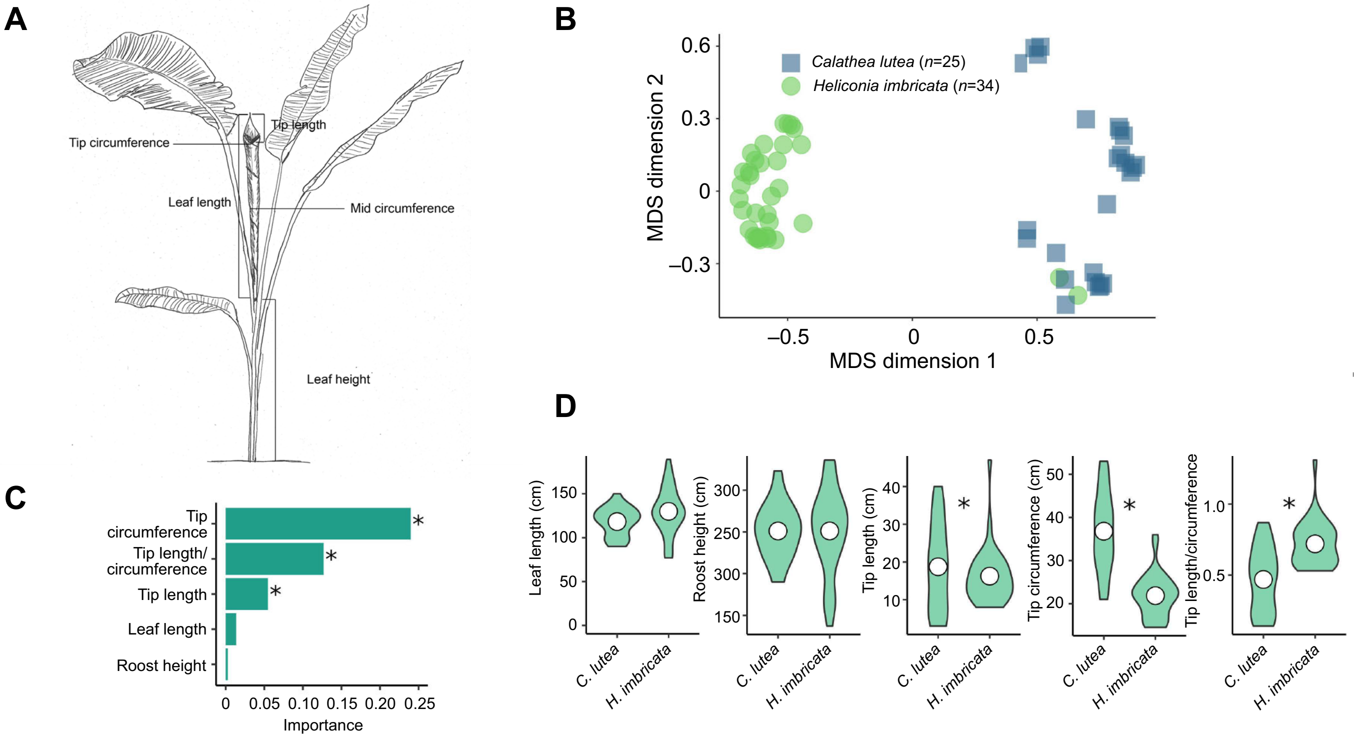

Fig. 1. Shape of leaves used as roost sites by *Thyroptera tricolor*. (A) Morphological parameters recorded from roosts. Tip circumference was measured at the tube opening, and mid-circumference was measured at the centre of the furled leaf (i.e. leaf length/2). In addition to these measures, we also calculated roost height – the sum of leaf height and leaf length – and available space – the difference between leaf length and tip length. (B) Leaf shape space based on the two dimensions of a multidimensional scaling (MDS) from the Random Forest proximity matrix. Sample size (*n*) represents the number of roosts measured; the same sample was used to generate C and D. (C) Random Forest importance (Gini impurity units) of the five variables used to classify furled leaves of *Heliconia imbricata* and *Calathea lutea.* Higher values imply a greater contribution for discriminating between the two species. (D) Violin plots comparing morphological variables between *H. imbricata* and *C. lutea*. Asterisks denote a significant difference in a given parameter between species, based on a randomization test on variable importance from the Random Forest classification model.

representing two vertical non-parallel planes, define a tri-dimensional space. We used the centre of the bats' head as a reference and located it for each time-lapse in a pair of synchronous video frames taken from both cameras at 60 frames s^{-1}. To locate the target accurately, we triangulated its position by analytic geometry and trigonometry. For that, we measured the two-dimensional coordinates of the target in each frame with PhysMo Video Motion Analysis v2.0, obtaining coordinates X_A and Z_A for camera A, and X_B and Z_B for camera B. We subsequently built the equations of the lines running from the focal point of each camera to the target position in each frame. The intersection of the two lines determines the tri-dimensional position of the target for each frame time. We comprehensively describe the mathematical procedure followed and the Microsoft Excel spreadsheet used for the calculations in Supplementary Materials and Methods. Finally, we built the flight trajectories of each bat from the frame-by-frame locations obtained with SketchUp (2016).

We characterized flight manoeuvres during two time periods prior to entering the leaf: the last inflection period (a variable period after the last inflection on the z-axis) and the ballistic descent period (a fixed period of 11 ms before landing, as described by Boerma et al., 2019). We measured four parameters at the start of each period: height, acceleration, distance to the leaf's opening and vertical angle. We also included the number of height inflections during the ballistic descent period. Differences in leaf landing manoeuvres between acuminate and truncate leaves were evaluated using supervised Random Forest (Breiman, 2001) on the described parameters. We used a Monte Carlo randomization approach (e.g. randomization that does not necessarily generate all possible combinations; Robert and Casella, 2010) to test the statistical significance of the Random Forest classification. To do this, we built a routine of shuffling the leaf-type categories to unlink them from any structure in the parameter data and calculated the out-of-bag (classification) error, which was replicated 10,000 times. Classification errors obtained from the randomization procedure were then compared with the observed value on the original dataset. We calculated the P-value as the proportion of expected random values lower than the observed value (i.e. how likely it was to obtain the observed classification by chance). In addition, we evaluated differences in multivariate variance in the flight manoeuvres for the two apex shapes using an analysis of multivariate homogeneity of group dispersions (Anderson, 2006) in the R package vegan (Dixon, 2003).

Landing performance

To determine whether the presence of a conspicuous leaf tip facilitates landing, we registered the landing patterns of 38 individuals onto acuminate and truncate tubular leaves. For this, we allowed bats to fly inside a flight cage for a maximum of 5 min or until they entered a leaf. The individual bats were tested on each leaf type once. The order in which the leaf types were presented to bats was randomized each day. For example, the first day, all bats were presented first with acuminate leaves and, upon successful completion of the task (i.e. entering the leaf), were tested later that same day with truncate leaves; the same process was reversed the next day: first set of trials with truncate leaves and then with acuminate leaves. Landings were recorded with a GoPro Hero7

Black camera (GoPro Inc.) in linear FOV (field of view) mode and at 60 frames s^{-1}. Videos of bats' landings were analysed to determine: (1) whether bats landed first with the thumb discs and then attached the foot discs (Boerma et al., 2019); and (2) the time elapsed since the bat made first contact with the leaf until it descended beyond the leaf's rim (hiding latency). We believe the latter is relevant as it estimates how long it takes the bat to become inconspicuous to potential predators. For the former, landings that followed that pattern were considered 'normal', whereas those that did not were considered 'odd'. For this set of experiments, we also decided to exclude juveniles and pregnant or lactating females; these criteria were established before the onset of experiments.

A Bayesian generalized regression model was used to assess whether the landing pattern (normal or odd) was associated with apex type (acuminate or truncate). Bernoulli distribution and a logit link function were used to model the response variable. We also evaluated the link between apex type, landing pattern and hiding latency. For this, we used Bayesian mixed model regressions with hiding latency as the response variable, individual as a mixed factor, and either apex type or landing pattern as predictors. A single multiple regression model was not evaluated as the two predictors were found to covary (see Results), which precludes inferring their effect on the third variable in a single model.

Statistical analysis specifications

Supervised Random Forest models (Breiman, 2001) were run using the R package ranger (https://CRAN.R-project.org/package=ranger). Optimal tuning parameters for Random Forest models were estimated in the R package tuneRanger (Probst et al., 2019), using 10,000 trees and 1000 iterations. All parameters were Box–Cox transformed before analysis, and highly collinear variables were excluded (mean absolute correlation to other variables higher than 0.9). Out-of-bag error (the mean prediction error on each sample using only the Random Forest trees that did not have that sample) was used as a classification performance metric. Random Forest importance was used to assess the relative importance of predictors, and importance was calculated using Gini impurity (Breiman, 2001).

All regression models were run in Stan (version 2.28.0; https://mc-stan.org/users/documentation/) through the R platform (http://www.R-project.org/) using the R package brms (Bürkner, 2017). All continuous predictors were z-transformed to remove differences in magnitude and simplify interpretability. We present effect sizes as median posterior estimates and 95% credibility intervals (CI) as the highest posterior density interval. Parameters in which credible intervals did not include zero were regarded as affecting the response variable. We applied a model averaging approach for parameter estimation on plant species preference, in which several models were evaluated. We used the Bayesian leave-one-out information criterion (LOOIC; Vehtari et al., 2017) with the R package loo (https://CRAN.R-project.org/package=loo) to assess the relative support of models to the data. LOOIC weights, which quantify the relative support compared with other candidate models, were then used to calculate weighted estimates averaged across models (i.e. model averaging).

All models were run on three chains for 30,000 iterations, following a burn-in of 3000 iterations. The adequate sample size was kept above 3000 for all parameters. Performance was checked visually by plotting the trace and distribution of posterior estimates for all chains. We also plotted the autocorrelation of successive sampled values to evaluate the independence of posterior samples. The potential scale reduction factor was used to assess model convergence and kept below 1.05 for all parameter estimates.

RESULTS

Our systematic surveys recorded 2715 furled leaves comprising seven plant species: *Calathea inocephala*, *C. lutea*, *Heliconia*

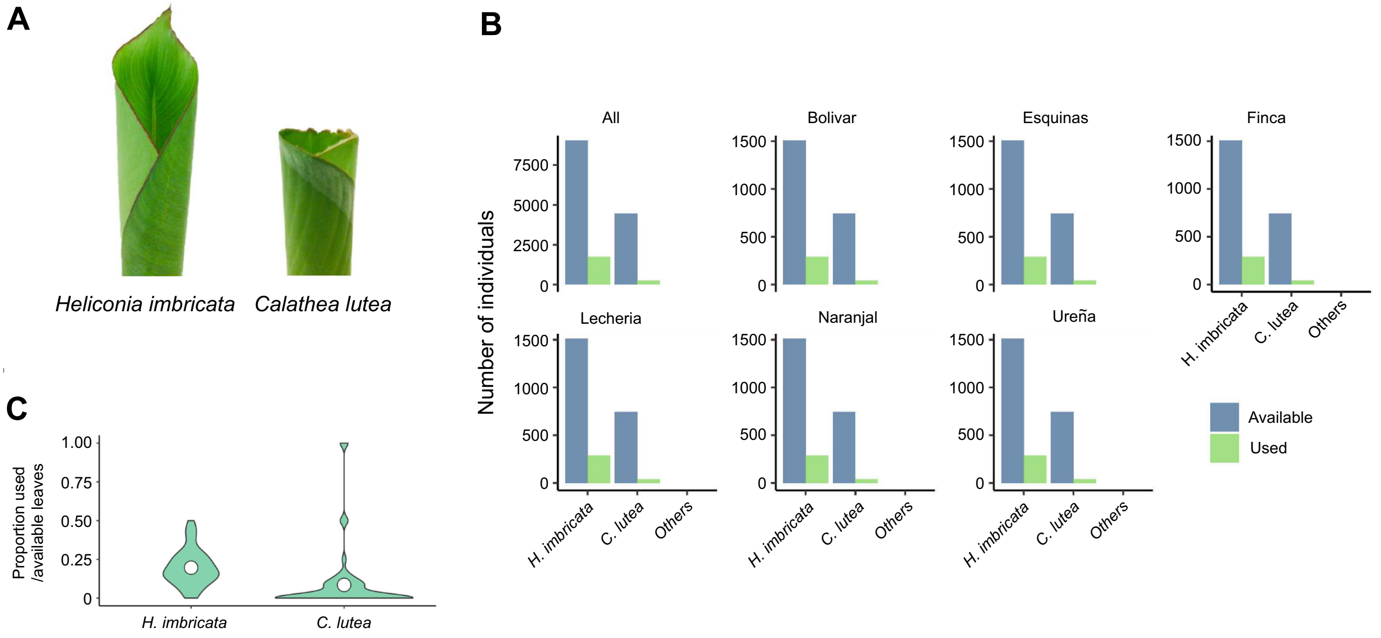

Fig. 2. Plant species preferred as roost sites by *T. tricolor*. (A) Photographs of the two most commonly selected plant species, *Heliconia imbricata* and *Calathea lutea*. (B) The number of used and unused (available) furled leaves per plant species. Detailed results are presented only for the two most commonly used plant species, while less commonly used plants are grouped into the single category 'others'. Data are shown for each of the six study sites separately and also collectively. Plant species significantly predicted whether bats used a given roost (effect size: 1.30; credibility interval, CI: 0.94–1.66), based on a Bayesian generalized linear model. (C) Violin plots showing the proportion of used per available furled leaves (greater values show that a specific plant species was used in a higher proportion for roosting according to its availability). Results are based on 104 sampling events at our six study sites.

imbricata, *H. irrasa*, *H. latispatha*, *H. stilesii* and *Musa* sp. The most commonly used plants for roosting were *H. imbricata* and *C. lutea* (Fig. 2A). These two species were the most commonly recorded plants with furled leaves (Fig. 2B). However, furled leaves were most commonly observed in *H. imbricata* at all sites. Plant species, but not plant density, significantly predicted the usage of furled leaves as roosts by *T. tricolor* across sites (Fig. 2C; species effect size: 1.30, CI: 0.94–1.66; density effect size: 0.0003, CI: −0.01–0.01). Bats preferred to roost inside *H. imbricata* leaves.

A Random Forest model classified the furled leaves of *H. imbricata* and *C. lutea* with an out-of-bag error of 3.38% (i.e. 96.6% correctly classified), indicating leaf shape differences between the two species (Fig. 1B). Only leaf tip parameters (tip circumference, tip length to tip circumference ratio, and tip length), but not overall leaf parameters (leaf length and roost height), contributed significantly to species discrimination (Fig. 1C,D). Most notably, after controlling for leaf circumference, leaves had a longer apex in *H. imbricata* (Figs 1D and 2A).

Flight trajectories of bats were classified according to the apex type of the leaves they were landing on for 73.7% of the trials (Random Forest out-of-bag error of 26.3%), and this classification was significantly higher than expected by chance (*P*=0.006). The multivariate variance was significantly higher on flight trajectories from experiments using truncate leaves (*F*=6.80, d.f.=1/36, *P*=0.0132; Fig. 3A). The landing pattern was associated with the apex type. Odd landings were estimated to be more than 3 times more common in truncate than in acuminate furled leaves (Fig. 3B; effect size: 3.28, CI: 1.01–6.23). We detected no effect of landing pattern (effect size: 205.51, CI: −88.54–495.01) or apex type (effect size: 31.52, CI: −245.13–306.49) on latency to hide (Fig. 3C).

DISCUSSION

Our study shows that *T. tricolor* exhibited a significant preference for furled leaves of *H. imbricata* over those of *C. lutea*, the two most common plant species sampled at our study sites in southwestern Costa Rica (Fig. 2). This preference is not related to overall availability. However, it could be linked to morphological differences between the furled leaves produced by these two species. The most conspicuous morphological differences between the roosts selected in these two plants correspond to the space used for landing when bats reach the roost: length of the leaf's apex (longer in *H. imbricata*), the leaf's width (broader in *C. lutea*), and the relationship between these two characteristics (Fig. 1).

The observed differences in morphology between the two plants most commonly used by *T. tricolor* may affect bats in two different ways. A narrow leaf probably allows bats to remain inconspicuous to diurnal predators that search for bats from above, such as monkeys and several species of birds of prey (Boinski and Timm, 1985), as less light will enter the tube, and bats usually roost at the bottom. Given that avoiding predation is of utmost relevance, it makes sense that tip circumference is the main characteristic preferred by bats when selecting roosts. However, this trait alone cannot explain the bats' preference for roosting in *H. imbricata*, as narrow leaves are available in both species. Another possibility is that bats select plant species that provide a longer-lasting tubular structure, thus decreasing the energy and predation costs involved in the location of a new roost during the daytime. Previous studies show that tubular leaves in some *Heliconia* species, compared with those in *Calathea* species, last longer (up to 31 h) within the bats' preferred circumference (ca. 22.30 cm; Vonhof and Fenton, 2004; Pérez-Cárdenas et al., 2019). However, tubular leaves in *Calathea* species might still be available within the bats' preferred circumference for

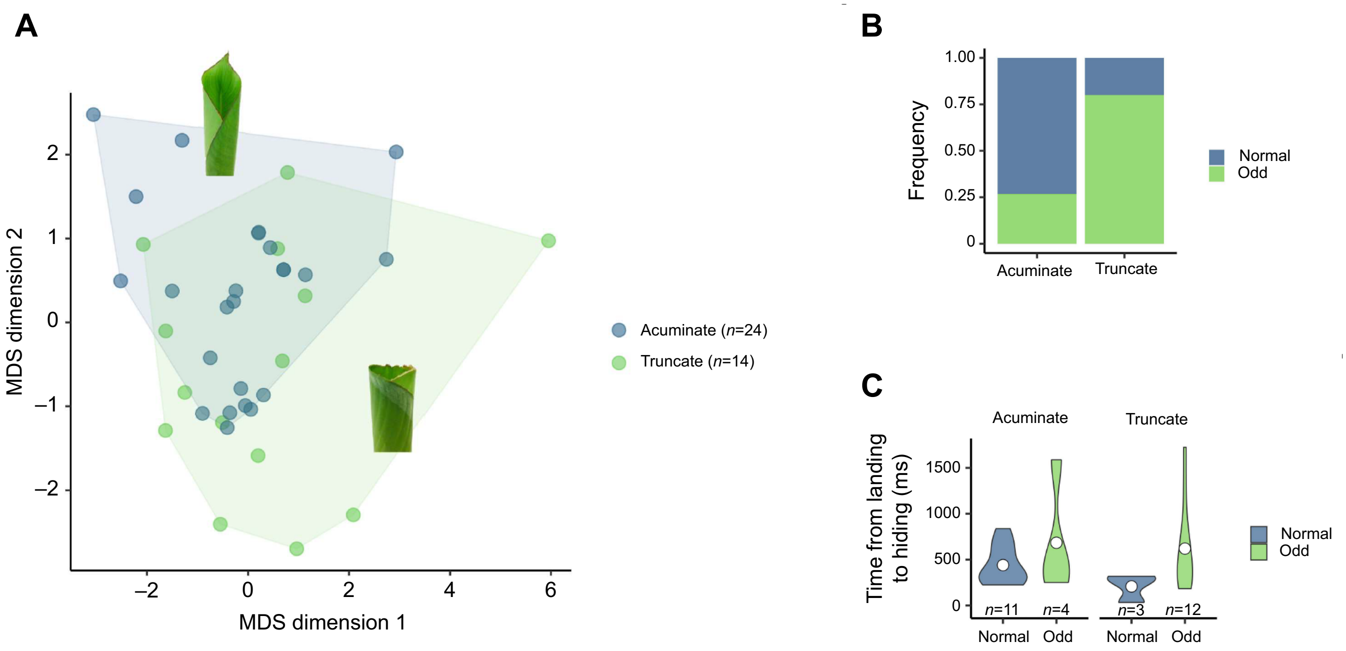

Fig. 3. Flight manoeuvres and landing performance while approaching and entering leaves. (A) Dispersion of estimated flight trajectories during approaches towards acuminate and truncate leaves (photos of each type are shown), projected using the two MDS vectors from the proximity matrix output from the Random Forest classification model. Sample size (*n*) represents the number of bats tested, and each bat was only tested once. (B) The proportion of normal and odd landings on the tubular leaf types (acuminate or truncate) used in the experiments. A significant effect of leaf type was observed (effect size: 3.28, CI: 1.01–6.23), based on a Bayesian generalized regression model. See C for sample size. (C) Time elapsed since bats first made contact with the leaf's structure until they moved beyond the rim. No significant difference was observed among leaf types and type of landing (based on a Bayesian mixed model regression). Sample size (*n*) represents the number of bats; each bat was tested twice, once in each type of leaf.

up to 14 h (Vonhof and Fenton, 2004). Considering that *T. tricolor* changes roosts daily, this difference in roost longevity does not seem particularly significant in explaining the bats' preference for roosting in *H. imbricata*. Yet, it certainly seems to deserve further examination.

Another way plant morphology may influence bats is by determining how they should approach and land on tubular structures. *Thyroptera tricolor* has the challenge of rapidly entering a tubular structure whose opening is scarcely broader than the bat itself. An apex seemingly facilitates that, as bats typically contact there, aided by the suction of their discs. Bats land on the roost in various ways without an apex, including the first contact between the forearms (and other body parts) and the leaf's rim. While these odd landings do not seem to increase the time needed for bats to hide within the tubular structure (potentially avoiding being detected by predators), they might cause injuries. The impact force applied by *T. tricolor* upon landing on leaves is very significant (mean peak total impact force of 6.98 bodyweights), the strongest measured in bats to date (Boerma et al., 2019). This impact force could be enough to damage bones if the force is not dampened sufficiently or the direction of contact is not appropriate, so being able to land in a controlled fashion may be critical for a bat's safety. In this respect, it is well known that bones are more resistant to fractures when forces are applied longitudinally versus transversely (Behiri and Bonfield, 1989; Li et al., 2013), as occurs for forearm bones when *T. tricolor* lands in the usual way. Thus, the probability of bone fractures could increase if the bat's forearms land first on the leaf's rim as this would represent a transverse force. Also, slowing down upon entering the leaf, aided by the attachment provided by the suction discs onto the leaf's inner wall, could be important if other group members are already roosting within it. An apex presence may also allow bats to quickly confirm that they can land on this surface without hitting group mates.

The absence of an apex may also influence a bat's approach to the roost's entrance. We found that flight manoeuvres of *T. tricolor* differ depending on the apex morphology of the roost leaf and that manoeuvres were more variable when approaching truncate leaves (Fig. 3A). In many motor tasks, especially when these are dangerous or require a long learning period, animals exhibit highly stereotypical motor patterns and movement trajectories. Performance in a motor task is often facilitated by reducing variability in the actions required to conduct that task (Dhawale et al., 2017). Given the potential costs of abnormal landings, a more defined landing strategy for approaching acuminate tubular leaves could result in a lower risk of injury when approaching such roosts. Despite this, we still do not have sufficient evidence to clearly establish whether flight manoeuvres are explained solely by the presence of an acuminate apex. Other explanations, such as differences in how bats perceive the two types of roosts (see next paragraph), need to be explored further.

Our study did not explore whether acoustic signatures and conspicuousness of echo profiles differ between plant species selected for roosting in *T. tricolor*. These differences might create sensory conflicts that could affect both the approach and landing phases, and perhaps the overall selection of roosting structures as well, explaining some of our findings. Previous studies show that bats can distinguish differences in echo-acoustic properties of surfaces coarser than around 380 µm (Simon et al., 2014) and that they may be attracted to plant structures that act as ultrasound reflectors (Schöner et al., 2015; Simon et al., 2011; von Helversen and von Helversen, 1999). Conflicts in perceived echo profiles during our experiments could arise from differences in leaf surfaces between plant species, differences in the width of tubular structures, or the presence of a conspicuous structure such as the apex. We controlled for the first two factors in our experiment addressing flight manoeuvres while entering leaves as the roosts were made from the same material and had a very similar tubular width. In the experiment on landing performance, we controlled for differences in leaf width but not the other two factors. We also do not know whether differences in leaf surfaces among the two selected plant species are significant enough for bats to perceive them. The issue of leaf acoustics should be addressed in future studies if we wish to carefully disentangle the role of various constraints, including biomechanical and sensory, during roost-site selection in bats.

In conclusion, we postulate that both ecological and biomechanical constraints strongly influence roost-site selection in *T. tricolor*. Bats might select narrow leaves with a long apex not only to avoid being detected by diurnal predators while in the roost (which was not directly tested in our study) but also to reduce the potential biomechanical costs involved in entering leaves with no safe landing surface. These findings add another layer to understanding the species' complex interactions with the resources it requires for survival. We know that the degree of resource specialization is one of the main predictors of species' vulnerability to extinction (Colles et al., 2009; Harcourt et al., 2002; Munday, 2004; Sagot and Chaverri, 2015). *Thyroptera tricolor* is already known to be a highly specialized bat that only uses tubular leaves for roosting. Our current results show that the available plant species may also highly limit this species' distribution within that already narrow niche, and that biomechanics should be incorporated into resource selection studies, especially when complex manoeuvres are needed to acquire those resources.

Acknowledgements

We thank Silvia Chaves-Ramírez and Mariela Sánchez-Chavarría for assistance during field data collection. Julio Bustamante and Lilliana Rubí Jimenez provided valuable guidance during the research permit application. We also thank Ronald Villalobos for logistics support and the Centro Biológico Hacienda Barú for their continuous support of our research.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: G.C., M.A.-S., J.A.; Methodology: G.C., M.A.-S., J.A.; Formal analysis: G.C., M.A.-S., J.A.; Investigation: G.C., J.P.B., T.U.-E., M.P.-A., A.L.V., J.A.; Resources: G.C., J.A.; Data curation: G.C., M.A.-S., J.A.; Writing - original draft: G.C.; Writing - review & editing: G.C., M.A.-S., J.P.B., T.U.-E., M.P.-A., A.L.V., J.A.; Visualization: M.A.-S.; Supervision: G.C.; Funding acquisition: G.C., J.A.

Funding

This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

Data availability

The data and R code supporting this article is available from the figshare repository: https://doi.org/10.6084/m9.figshare.20186807.v2

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