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Home ranges, feeding sites, and daily movement behavior of the highly threatened Livingstone's fruit bat revealed through GPS tracking

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Abstract
The highly threatened Livingstone's fruit bat, *Pteropus livingstonii*, is endemic to only two islands of the Union of the Comoros, a country with some of the highest deforestation rates worldwide. The majority of the bat population is found on Anjouan, where only 10% of the island surface still has intact forest cover. Classed as a "forest-dependent" species, our aim was to understand the landscape use of the bats in order to focus conservation efforts on important bat resources. For this we retrieved movement data from 17 individuals fitted with GPS trackers between May 2022 and October 2023, in both the dry and the wet seasons. We identified home ranges, potential feeding sites, and daily movement behavior. Potential feeding sites were found mainly in forest and agroforest habitats, the two landcover classes with high tree cover. The tagged bats traveled similar distances during the day as during the night, indicating increased diurnal movement compared to closely related species, possibly due to a combination of lack of predation and having to meet nutritional needs in a highly degraded landscape. The results of this research will be integrated into a landscape-wide conservation programme implemented by a local conservation organization together with communities.

KEYWORDS
flying fox, forest-dependent, habitat loss, habitat use, Indian Ocean, island conservation

1 | INTRODUCTION

Forest loss disproportionately affects least developed countries and small island developing states within the Tropics, impacting critical ecosystem services such as carbon storage and biodiversity (Asner et al., 2010; FAO, 2020; Gibson et al., 2011; Mace et al., 2012). One of the drivers of deforestation is anthropogenic land-used change for urban development and agricultural intensification to meet resource needs (Foley et al., 2005). The modification and loss of tropical forest cover is predicted to impact the climate on a regional and global scale (Lawrence &

Vandecar, 2015; Mahmood et al., 2016; Medvigy et al., 2013; Werth & Avissar, 2002) and eliminates important habitat and resources for wildlife (Shackelford et al., 2018; Tulloch et al., 2016). Deforestation is directly linked to wildlife population decreases and even local extinctions (Kinnaird et al., 2003; Sodhi et al., 2010).

Large Old World fruit bats are some of the most endangered taxa in the world: over 70% of the described species are assessed as threatened by the International Union for Conservation of Nature (IUCN), with most of the species restricted to islands (Kingston et al., 2023). Unsustainable hunting is one of the major threats faced by these animals (Brook et al., 2019; Sheherazade & Tsang, 2015; Struebig et al., 2007), followed by loss of native forests, which is the natural habitat for many *Pteropus* and *Acerodon* species (Kingston, 2010; Kingston et al., 2023). Deforestation on small islands brings with it a reduction in carrying capacity, loss of roosting and important feeding resources, increased disturbance, and decreased resilience to climate change, all of which have detrimental effects on Old World fruit bats (Cousins & Compton, 2005; Jones et al., 2009).

The Union of Comoros, a small island nation located in the Mozambique channel, Western Indian Ocean, has seen a drastic reduction in forest cover since the 1990s, with around 80% of remaining natural forest lost between 1995 and 2014 (Boussougou & Brou, 2015). The Comoro islands are home to two species of Old-World fruit bat: the widespread and introduced Seychelles flying fox, *Pteropus seychellensis*, and the endemic Livingstone's fruit bat, *P. livingstonii*, which only occurs on the islands Anjouan and Mohéli. The Livingstone's fruit bat is by now one of the most endangered fruit bats in the world with only approximately 1500 mature individuals remaining (Daniel et al., 2017; Ibouroi et al., 2018; Mandl et al., 2024). The larger of the two populations (around 1300 individuals) is located on Anjouan which is simultaneously the island with the highest deforestation and highest human population growth of all three Comoro islands (Boussougou & Brou, 2015; Granek, 2002; Marsh et al., 2010). The majority of the 424 km^2 island is marked by small-scale agricultural fields and settlements (Doulton et al., 2015; Mandl et al., 2022). Very little is known about the Livingstone's fruit bats' ecological requirements: long-term roosts are generally located in areas with remaining forest fragments (Granek, 2002) and habitat suitability modeling suggested very little habitat remains for the species on both Mohéli and Anjouan (Ibouroi et al., 2018). While the known roost sites are surveyed regularly, little information is available on important feeding resources within the landscape, making it difficult to integrate feeding areas into conservation efforts to ensure the species' survival. Amidst these ongoing challenges, the bat population has remained stable over the past decade (Mandl et al., 2024), suggesting they may be able to cover their needs in the highly altered landscape (Aguiar et al., 2016; Bellard et al., 2012). The Comoros are an ideal case study to investigate animal–landscape dynamics on islands under high anthropogenic pressures. Understanding how highly mobile, forest-dependent island species such as fruit bats use landscapes that are fragmented and degraded can inform targeted conservation approaches world-wide. Their limited options for dispersal make island bats particularly vulnerable to habitat loss and learning how they survive in closed systems like Comoros can provide insights into which nature-based solutions should be prioritized to maintain healthy island ecosystems.

For this study we aimed to understand the species' use of landscape on Anjouan, to identify sites of conservation importance. Given their strong association with intact high-altitude rainforests, we hypothesized that the bats preferentially used forested areas for activities like feeding or roosting. Through GPS-tracking of bats for 16 months, we were able to identify home range locations, potential feeding sites, daily movement behavior, and preferred habitats across the island. The results will help inform ongoing landscape conservation efforts on Anjouan to ensure the species' resources are protected.

2 | METHODS

2.1 | Study site and capture

We collected data for this study between May 2022 and October 2023 on the second largest island of the Comoros Islands, Anjouan (12°12′54″S; 44°25′30″E), located in the Mozambique Channel. The Comoro islands show two distinct seasons: a hotter, wet season between November and April (average daytime temperatures of 32°C) and a colder, dry season between May and October (average daytime temperatures of 24°C). Anjouan has a highly mountainous terrain, with elevations up to 1500 m. The natural vegetation cover is rainforest, but high levels of deforestation have led to the decimation of most forest (Doulton et al., 2015). Only around 10% of the island is currently covered in degraded and intact forest fragments, often located on steep slopes and inaccessible areas (Dahari, 2021). We captured 30 bats using canopy-level mist nets (nylon, mesh size: 60 × 60 mm, ECOTONE, 81-583 Gdynia, Poland) at three locations near known feeding and roosting trees in May (3 nights, Moya), June (3 nights, Hombo), and September (4 nights, Salamani) 2022 as well as May (3 nights, Salamani) 2023. Mist nets were opened and constantly monitored between 1700 and 2200 h and again between 0300 and 0700 h during catching nights. When a bat was caught in the net, the net was lowered immediately and the bat was extracted, weighed and measured by experienced handlers wearing appropriate personal protective equipment (gloves, masks). Handling time was kept to a minimum to ensure both animal and human wellbeing and safety, and bats were not kept longer than necessary to finish all procedures. We equipped 22 bats (10 females, 12 males; see Data S1, Supporting Information for information on all tagged individuals) weighing more than 400 g (to ensure the tag did not exceed 5% of the bats' body weight; Aldridge & Brigham, 1988) with GPS tags weighing 15 g (Bird Solar, e-obs GmbH, 82931 Grünwald, Germany). The tags were attached to a handmade collar (faux leather and neoprene, closed with a dissolvable suture) designed to fall off after 4–6 months as recapture of the same individuals was unlikely. We retrieved three fallen collars during data collection as they continued to send GPS locations after having dropped near feeding and roosting sites. We were able to collect and analyze data from 17 individuals. The remaining five tags were lost within 48 h of tagging, or after only one data download.

2.2 | Data collection

Tags were programmed to collect both GPS and acceleration data: when the bats were moving with a speed of 50 cm/s, the tags recorded a GPS relocation every 90 s. When bats were stationary, the tags recorded a GPS relocation every 6 h. Acceleration data were collected for 4 s every minute across all three axes (16.7 Hz), allowing detailed insights into bats' movement, even if no GPS points were available. Tags switched off when the battery level fell below a certain threshold and switched on again if there was enough solar recharge. Recharging occurred during the sunny day as bats rested in exposed areas on tree branches. This programming resulted in non-regular GPS sampling throughout the study period but enabled insights into flight paths, resting, and potential feeding areas. Data were downloaded remotely via UHF radio communication from bats in roost sites multiple times per week during the study period using a handheld base station and antenna (e-obs GmbH, 82931 Grünwald, Germany).

2.3 | Analysis

2.3.1 | Home ranges and travel distances

We computed home ranges for all individuals as autocorrelated density kernel estimations (AKDE), using the "ctmm" (Fleming & Calabrese, 2023) package in R (R version 4.4.1, 2024-06-14) utilizing all available GPS relocations for each individual. We investigated the effect of sex on (log-transformed) home range size, controlling for the number of days data were collected using a linear mixed model with the package "lme4" (Bates et al., 2015). Daily travel distances of all tagged bats were extracted via QGIS (QGIS.org, 2024, QGIS Geographic Information System) using only GPS points taken before the battery levels were depleted for the first time: after initial battery depletion, sampling became too irregular to reflect true movements across the landscape as batteries rarely recharged enough to sustain data collection for prolonged periods of time, instead only sampling for a couple of hours per day before batteries depleted again. Travel distances were divided into 12 h periods: "night" from 6 p.m. to 5:59 a.m. and "day" between 6 a.m. and 5:59 p.m. to reflect bat activity patterns. We investigated the effects of daytime (night/day) and sex on the recorded travel distances using generalized linear models with the package "nlme" (Pinheiro et al., 2024), for which we set daytime and sex as fixed effects and the individual id as a random effect to control for inter-individual variability.

2.3.2 | Landscape use and potential feeding sites

We identified potential feeding sites in the bats' home ranges by annotating all available GPS points into behavioral categories extracted from the associated acceleration data using the FireSOM algorithm inbuilt in Firetail® (Firetail v12.2.0, Schäuffelhut Berger GmbH, Unterhaching, Germany). The FireSOM algorithm assigns categories to each acceleration data burst: categories are based on the similarities of the selected XYZ axis statistics of the acceleration data (minimum, maximum, median) and the overall dynamic body acceleration (ODBA) recorded by the tag. The categories are validated manually and assigned a behavior based on previous field and zoo observations (behavior of three tagged individuals was recorded for a set amount of time and cross-referenced with the acceleration data). This allowed for annotation of all GPS points into one of the following basic categories: "Flying"—the bat is airborne, "Resting"—the bat is stationary on a tree and not moving, often asleep, and "Moving/Climbing"—the bat is on a tree or branch, mobile and moving its body, either stationary or climbing between branches. We then extracted all GPS points in the "Moving/Climbing" category as this was the only time GPS points could have been collected during feeding events, indicating potential feeding locations. The "Moving/Climbing" GPS points were then analyzed using a DBSCAN analysis in R (Hahsler et al., 2019), with a minimum selection of five points per cluster. We drew minimum convex polygons around each of the resulting clusters (="potential feeding sites") and calculated the proportional landscape composition of the clusters between individuals using a landcover classification map of Anjouan. As Anjouan's small size meant that the bats potentially had access to the entire island within the data collection period, we did not restrict the landscape comparison to certain parts of the island only.

We also investigated whether the tagged bats chose higher elevations and steeper slopes disproportionately. For this we compared true GPS relocations of 15 individuals (two individuals were excluded from this analysis as we had less than a week's worth of GPS tracking data available from them) to random GPS relocations generated from the bats' tracks (created using the "amt" package in R; Signer et al., 2019). We computed a general linear mixed model with elevation and slope as fixed effects for true and random GPS relocations and included bat id as a random effect to control for inter-individual differences. Model fit was validated using diagnostic plots and the magnitude of the effects (or mean ± SE) were visualized as tree plots in "sjPlot" (Lüdecke, 2024).

2.4 | Ethical approval and permits

All project procedures were carried out with ethical approval from the Animal Ethics and Experimentation Board, Faculty of Life Sciences at the University of Vienna (No. 2021-023). Permission to conduct the research in collaboration with the NGO Dahari and the University of Comoros was granted by the Comorian government under permit No. Ref/01/2018.

3 | RESULTS

3.1 | Home ranges and travel distances

We retrieved sufficient data for analysis from 7 females and 10 males. Mean(±SE) size of 95% AKDE home ranges was 11.87 ± 15.1 km^2 for females (min: 0.88 km^2, max: 43.75 km^2) and 11.75 ± 14.2 km^2 for males (min: 2.05 km^2, max: 47.63 km^2). There was no significant difference in home range size between the sexes ($F_{(1)} = 0.07$, $p = .7$) (Figure 1).

A similar picture emerged with travel distances: the number of days we were able to extract paths varied between individuals (due to battery life, min: 3, max: 37 days) but there were no significant effects of daytime or sex on the traveling distance (daytime: $F_{(1)} = 2.05$, $p = .15$; sex: $F_{(1)} = 0.94$, $p = .34$; daytime and sex: $F_{(1)} = 1.07$, $p = .29$). Although the results showed no statistical significance, the tagged bats traveled slightly further at night (6 p.m.–5:59 a.m.), with a mean distance of 4.3 ± 2.8 km, than during the daytime (6 a.m.–5:59 p.m.) with a mean of 3.9 ± 3.1 km. Females traveled on average 4.6 ± 3.1 km during the day and 4.7 ± 2.9 km during the night, while male mean travel distance was 3.6 ± 3.1 km during the day and 4.1 ± 2.8 km during the night (Figure 2). The minimum distance traveled by a male at night was only 119 m, while the maximum was 17.9 km. For female bats the minimum distance traveled at night was 647 m, while the maximum distance was 16.9 km.

Most tagged bats switched roosts at least once, with six bats visiting at least three roost sites within the study period. However, the relatively short daily traveling distances can be attributed to the bats remaining within 1–2 km of the area of the sites they were originally caught in, with exploratory flights (over 20 km in length; Banack & Grant, 2002) happening infrequently during the study period (Figure 2).

3.2 | Landscape use and potential feeding sites

The number of potential feeding sites identified in the dataset varied between individuals with a minimum of 6 to a maximum of 30 sites per individual. The mean size of a potential feeding site was 5.8 ± 17.1 ha based on the size of the calculated polygons. The landscape composition of the potential feeding sites was varied: all bats visited agricultural lands, agroforest (landscape with a mix of non-indigenous trees and agricultural activities), and forested areas, but to varying degrees. Three individuals (two males and one female) visited nearly exclusively forested areas during the study period and the potential feeding sites of four bats covered human settlements (towns, villages), but at a minimal level. Less than 0.1% of the bats' potential feeding sites comprised areas classified as settlements and fallow soil. They consisted of around 55% forest, 35% agroforest, and 10% agricultural land area (Figure 3). In comparison to the available landcover on Anjouan as a whole, forest was selected disproportionately to availability. Around 40% each of the island is comprised of agricultural land and agroforest, with only 10% of the island covered in forest.

Most of the remaining forest is found on higher elevations and steeper slopes (Dahari, 2021). The results of the GLM indicated that the tagged bats preferentially passed through areas with steeper slopes (standard error (SE) = 0.004, $z = 31.9$, $p < .01$), and at higher elevations

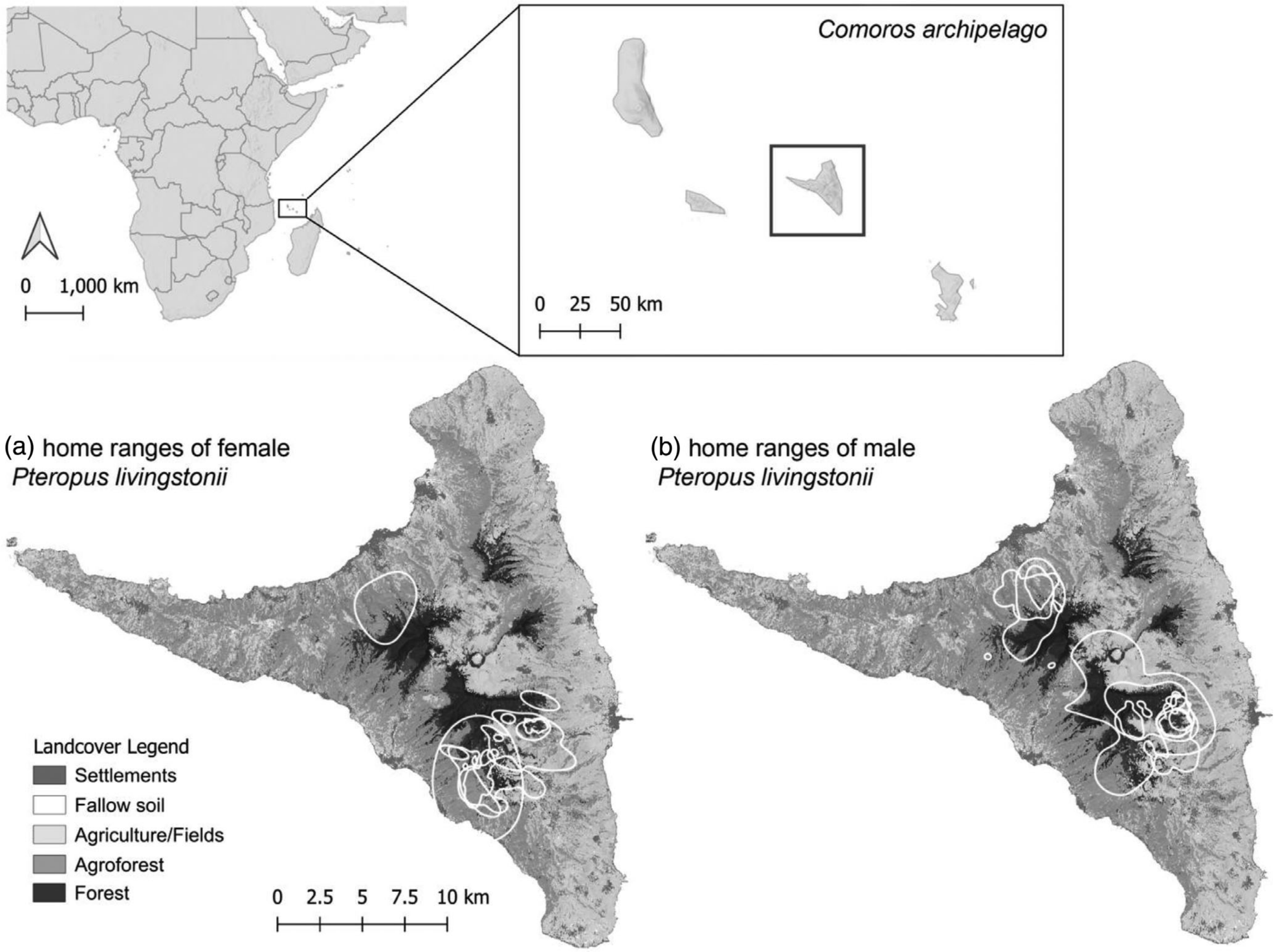

FIGURE 1 Map of study site (Anjouan, Comoro islands) with home ranges of female (a) and male (b) *Pteropus livingstonii* GPS-tagged between May 2022 and October 2023. Landcover map created using Sentinel 2 images (Dahari, 2021): forested areas total to 46.5 km^2, agroforests (areas with introduced and non-native trees, as well as agricultural activities) 169.6 km^2, agricultural fields 178.4 km^2, fallow soils (non-cultivated ground) 6.9 km^2, and settlements 23.8 km^2.

($SE = 0.005$, $z = 3.8$, $p < .01$) but the interaction between elevation and slope ($SE = 0.004$, $z = 1.1$, $p = .2$) had no significant effect on where the bats chose to go.

4 | DISCUSSION

This was the first long-term study to use high-resolution GPS data to provide detailed insights into the space use of the highly threatened Livingstone's fruit bat, *Pteropus livingstonii*—specifically home ranges, movement patterns, and potential feeding sites. We found that the bats were active during daylight hours, traveled short distances, and mainly sought forested areas for potential feeding.

The tagged bats traveled shorter distances compared to a few similarly sized species (Banack & Grant, 2002; Oleksy et al., 2019). Except for two individuals which moved between the north and the south of the island, the tagged bats remained within a few kilometers of their original capture locations near long-term roosts. The estimated home ranges of the bats were comparable to those of other island flying foxes, including Japanese and Malagasy species (Nakamoto & Kinjo, 2012; Oleksy et al., 2015), but in contrast to those species no differences could be detected between male and female home ranges. The two roost sites furthest from each other on Anjouan are 15 km apart, which makes all known roosts easily accessible within a single night to *Pteropus* bats, capable of flying more than 80 km at a time (Welbergen et al., 2020). Indeed, we found that most of the tagged bats switched roosts multiple times during the study period, mainly visiting other sites located within a 4-km radius of their capture site—with flights between sites occurring both during the day and the night. Overall, the studied bats were very active during daytime hours

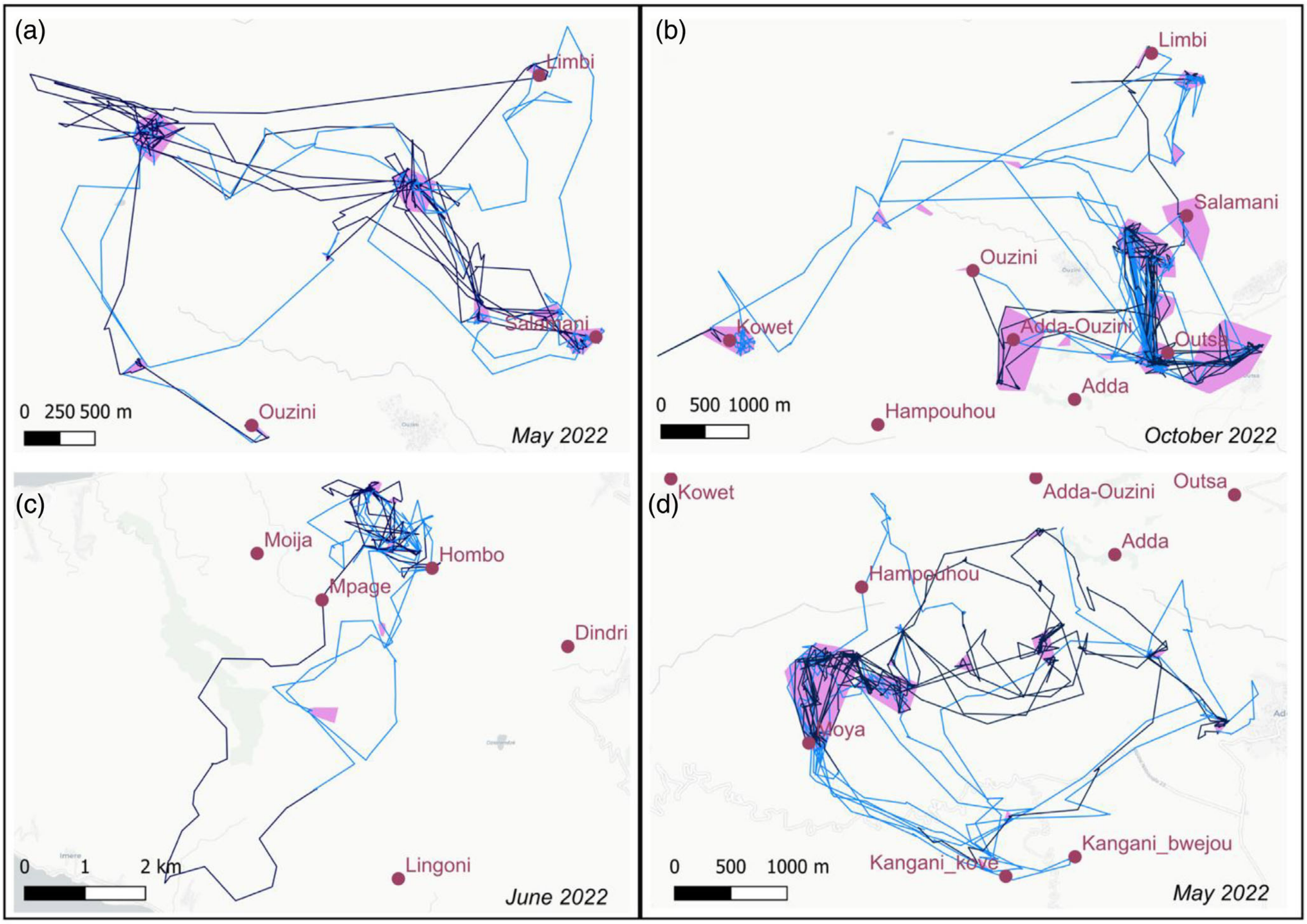

FIGURE 2 Movements of four *Pteropus livingstonii* individuals on Anjouan, Comoros, recorded between May and October 2022: (a, c) male tracks, (b, d) female tracks. Light colored paths indicate movements between 6 a.m. and 5:59 p.m. (day), dark paths between 6 p.m. and 5:59 a.m. (night). Pink polygons indicate potential feeding sites, extracted from GPS and acceleration data between May 2022 and October 2023. Dots with labels represent known long-term roost sites on Anjouan.

(6 a.m.–6 p.m.), traveling about the same distance as during the night. This contrasts greatly with most other flying fox species that remain stationary, asleep for the majority of the time, during the daytime and only exit their roosts at sunset, such as *P. policephalus* in Australia, *P. vampyrus* in Indonesia, and *Acerodon jubatus* in the Philippines (Connell et al., 2006; Hengjan, Iida, et al., 2017; Hengjan, Pramono, et al., 2017). Increased daytime movement and early roost emergence in *Pteropus* is potentially costly as animals are required to trade-off between increased predation risks and foraging needs, with individuals with higher foraging needs (i.e., lactating females) often leaving roosts earlier (Eby, 1991). Predation, including hunting pressure by humans, can delay roost emergence as bats wait for darkness before heading out to forage (Hengjan et al., 2018). On Comoros, there is little predation pressure as bats are not hunted. In addition, there are no recorded observations of birds of prey (*Circus macrosceles*, *Accipiter francesii*, *Tyto alba*, *Buteo buteo*) predating on *Pteropus* on the islands. As a result there are likely fewer risks associated with leaving the roost earlier during the day. However, the increased movement during the day by the Livingstone's fruit bats may be attributed to increased foraging needs in a highly altered landscape: bats need to maximize their available active time to meet nutritional demands (Hengjan, Iida, et al., 2017; Hengjan, Pramono, et al., 2017). Similarly, the short distances traveled, and staying within a 4-km radius around roost sites, may reflect their need to minimize commuting distances in attempts to decrease energy expenditure (Lewis, 1995). In contrast, the widespread and introduced co-occurring Seychelles flying fox, *P. seychellensis*, typically starts leaving their roosts at sundown (Trewhella et al., 2001), potentially highlighting different factors influencing both species.

We identified areas that indicated potential feeding sites based on acceleration data collected by the GPS tags

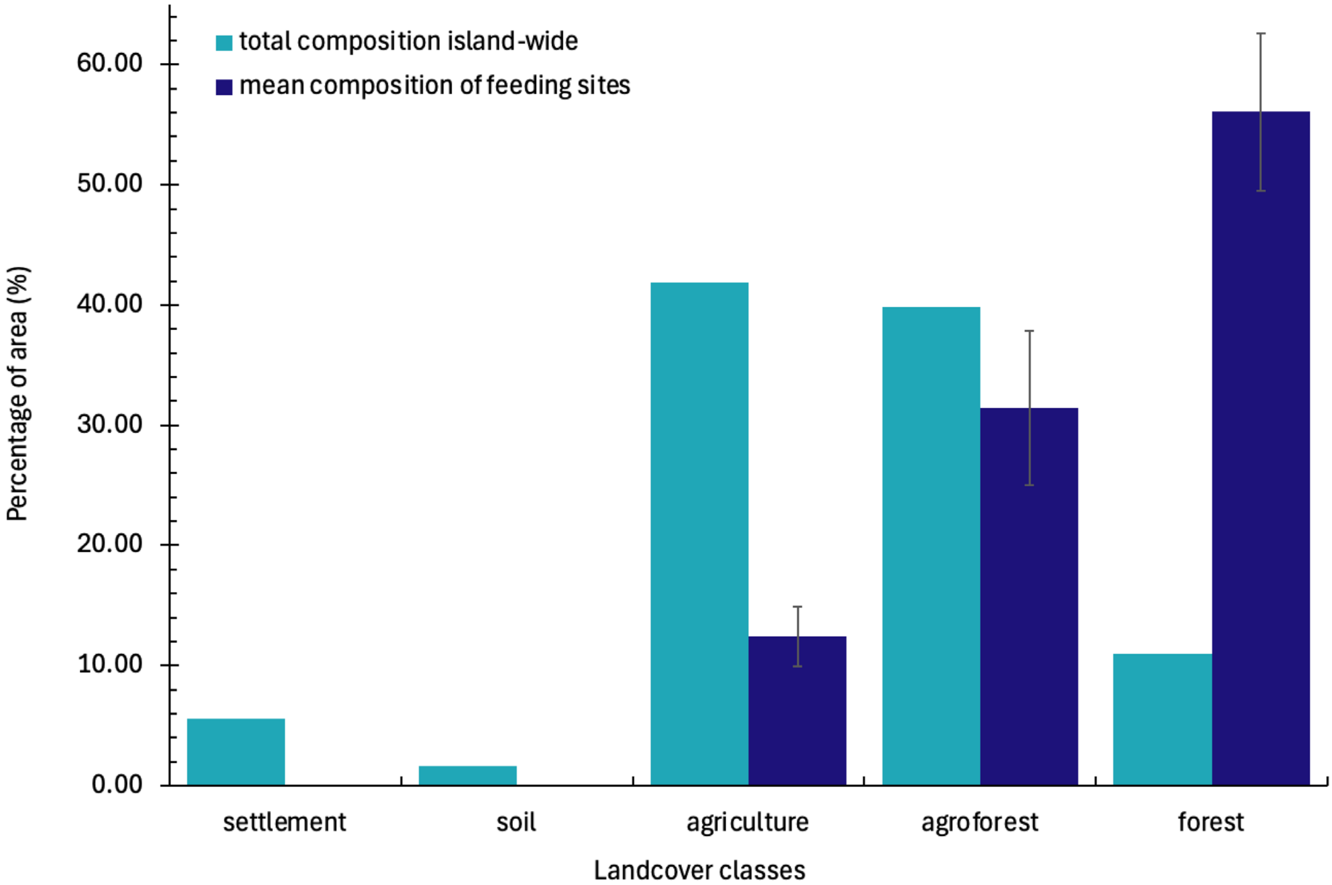

FIGURE 3 Comparison of landscape composition of Anjouan island, Comoros (light blue), to the mean composition of potential feeding sites ($N = 238$) of *Pteropus livingstonii* individuals between May 2022 and October 2023 (dark blue). Error bars represent the standard error around the mean.

which indicated behaviors corresponding to feeding. The majority of those sites were located around or near known long-term roosts. The average identified feeding site of the tagged bats was comprised of over 50% forest and over 40% agroforest, but sites varied considerably in their landscape composition across the dataset, with some bats remaining exclusively in forest, while others visited mainly agroforest. The landscape categories used in this study are broad, because of the coarse resolution imagery used to create the landscape map: it is possible that within the named categories nuances may exist that influenced the bats' choice of landscape cover. Overall, when compared to the full range of habitats available across the island of Anjouan, the bats showed a clear preference for visiting forests and agroforests. They also remained in areas with steeper slopes and higher elevations. However, as most of the remaining natural forest is now concentrated in these elevated and steep regions (Dahari, 2021), these preferences cannot be considered in isolation. It is likely that the bats selectively targeted the remaining forested areas, subsequently spending more time at higher elevations and on steeper terrain. Interestingly, the GPS locations of the tagged bats in this study overlapped very well with a habitat suitability model published in 2018 that highlighted remaining suitable habitat to be in high-elevation forested areas and on steep slopes (Ibouroi et al., 2018). Similar findings have been reported for the large flying fox, *P. vampyrus*, and the giant golden-crowned flying fox, *A. jubatus*, in the Philippines, where both species chose natural forest areas disproportionately to other landcover types (Mildenstein et al., 2005). In Japan the Ryukyu fruit bat, *P. dasymallus*, chose areas with more forest and less anthropogenic interference (Lee et al., 2009), and Mauritian flying foxes, *P. niger*, preferred natural forests if undisturbed (Oleksy et al., 2019; Seegobin et al., 2022). While only around 10% of Anjouan's land is covered in forest fragments (of varying degradation), about half of the island has considerable tree cover through agroforestry (agricultural practices incorporating tree cultivation; Harvey & González Villalobos, 2007). On Anjouan, all accessible areas show some degree of anthropogenic influence (Doulton et al., 2015; Mirhani et al., 2019) and only agroforestry areas and forests still have the extensive tree cover important for the survival of *Pteropus* species (Frick et al., 2020). In our study a considerable portion of the tagged bats' home ranges and potential feeding sites fell into agroforest landscape suggesting that *P. livingstonii* is able to find resources in this human-impacted landcover class, possibly because agroforests harbor a mix of native and non-native vegetation and introduced trees that are found to be feeding plants for *Pteropus*, such as *Ceiba pentandra* and *Artocarpus* sp.

The biggest drivers of endemic island species extinctions are hunting, habitat loss, and invasive predators (Wood et al., 2017). In the case of the Livingstone's fruit bat, the species is sufficiently mobile to cross non-forested areas in a fragmented landscape, as well as potentially substituting lost feeding and roosting resources in agroforestry landscapes. Anjouan presents a rare example where the habitat loss due to anthropogenic pressure occurs without the pressures of hunting and invasive predatory species. The combination of these threats usually requires comprehensive conservation approaches for *Pteropus* bats, to address the socioeconomic and cultural drivers behind them (Kingston et al., 2023). Many bat species seem to adapt to these threats to some extent, but small island species may have difficulties finding alternatives. Across the globe more generalist *Pteropus* species show adaptations in foraging and roosting habitats in response to changing landscapes: gray-headed flying foxes increasingly use urban areas in Australia for both feeding and roosting (Boardman et al., 2021; Meade et al., 2021; Páez et al., 2018). Similarly, Ryukyu's fruit bats feed on introduced fruit trees in urban areas (Nakamoto et al., 2007). Both Lyle's flying fox, *P. lylei*, and the Pacific flying fox, forage mostly on farmland, but require intact mangroves and forests, respectively, for survival (Luskin, 2010; Weber et al., 2015). In Bangladesh, as more habitat is converted to farmland or urban areas, Indian flying foxes, *P. medius*, shifted to smaller colonies roosting closer to humans (McKee et al., 2021). This species seems to generally adapt well to human presence, if enough feeding resources are available (Hahn et al., 2014; Jeyapraba, 2016).

The native rainforest on Comoros has undergone extensive deforestation, and efforts are in place to protect the remaining forest fragments as well as restore areas of conservation importance (Dahari, 2024). The NGO Dahari is working directly with landholders on Anjouan to trial a "conservation agreements" approach: the agreements incentivize forest restoration in areas which benefit endemic biodiversity and water provisioning. The results of the current study will be integrated into this approach, informing which areas are important for the conservation of Livingstone's fruit bats. Since 2015, individual landowners with roost trees on their properties have been offered incentives—such as training in sustainable, profitable agricultural techniques and in-kind payments—to preserve these trees. This approach has helped ensure the long-term protection of these critical resources. The bat-related conservation efforts on Comoros are geared towards protecting the remaining natural habitat for the bats, as well as restoring some of which has been lost. As the most concerning threat is habitat loss, and the bat population is stable, albeit small (Mandl et al., 2024), this approach may be sufficient to prevent extinction of the species. This study provided critical information to optimize landscape-scale restoration work to inform bat conservation. To ensure long-term success in saving the species from extinction continued monitoring of the population, as well as regular assessments of the state of the island's forests are required.

5 | CONCLUSIONS AND CONSERVATION IMPLICATIONS

The results of this study revealed important ecological information about the highly threatened Livingstone's fruit bat, a species endemic to the Comoro Islands. The bats preferred forested areas found in high elevations and steep slopes on Anjouan island, with their potential feeding sites being located in natural forest and agroforest landcover. Unlike many other studied *Pteropus* species the Livingstone's fruit bats showed high daytime activity levels and short daily travel distances within their ranges. Their behavior could reflect difficulties in meeting nutritional needs in the highly altered landscape of Anjouan (higher activity levels during the day, short commuting distances as bats stay in proximity to potential feeding resources). However, more research into the bats' dietary ecology is needed to understand these dynamics.

The results of the study highlight areas that likely harbor important feeding resources for the Livingstone's fruit bats as a basis to inform active conservation actions on the island. Moving forward, local landholders are incentivized by the Comorian NGO Dahari to protect important bat areas amidst larger landscape-wide restoration efforts. These actions aim to preserve bat habitat on Anjouan for the species' survival.

As island biodiversity faces widespread habitat loss on a global scale, this study represents an interesting case of how such processes affect endemic fruit bats and highlights how research can be applied to inform conservation efforts.

AUTHOR CONTRIBUTIONS

IM designed the project, collected and analyzed the data, and wrote the manuscript. BBAA and IS implemented the project and collected the data throughout the study period. TOM performed the statistical analysis and provided input to the manuscript. JF oversaw project implementation and provided editorial input to the manuscript. SSAC oversaw project implementation and facilitated permitting processes. OL oversaw the creation of landscape maps and provided input into the manuscript. MM oversaw project implementation and fieldwork. HD co-designed the project, oversaw fieldwork and data analysis, and provided input into the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available upon reasonable request but due to the sensitivity of the data (GPS relocations of highly threatened species) all requests will be vetted carefully.

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SUPPORTING INFORMATION

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

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