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Greater spear-nosed bats commute long distances alone, rest together, but forage apart

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Animals frequently forage in groups on ephemeral resources to profit from social information and increased efficiency. Greater spear-nosed bats, *Phyllostomus hastatus*, develop group-specific social calls, which are hypothesized to coordinate social foraging to feed on patchily distributed balsa flowers. To test this, we tagged all members of three social groups of *P. hastatus* on Isla Colón, Panamá, using high-frequency GPS during a season when balsa had begun to flower. We found that bats commuted 20–30 km to foraging sites, more than double the distance reported previously. In contrast to our expectations, we found that tagged individuals did not commute together, but did join group members in small foraging patches with high densities of flowering balsas on the mainland. We hypothesized that close proximity to group members would increase foraging efficiency if social foraging were used to find flower clusters, but distance between tagged individuals did not predict foraging efficiency or energy expenditure. However, decreased distance among tagged bats positively influenced the time spent outside roosing caves and increased the duration and synchrony of resting. These results suggest that social proximity appears to be more important during resting and that factors other than increased feeding efficiency may structure social relationships of group members while foraging. It appears that, depending on the local resource landscape, these bats have an excellent map even of distant resources and that they use social information only for current patch discovery, and thus, they do not appear to rely on social information during daily foraging.

Keywords:
energy expenditure
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social behaviour

Animals must respond to changes in the spatiotemporal distribution of resources to satisfy their dietary requirements, and thus, their movement decisions to search for and exploit food resources directly impact their fitness (Bell, 1990). When resources are ephemeral (e.g. spatially patchy, temporally unpredictable), using social information while moving with others may help them find resources more efficiently (Bhattacharya & Vicsek, 2014). For example, fish track moving refuges by matching speed to groupmates (Berdahl et al., 2013), insect- and fish-eating bats converge on the feeding calls of conspecifics (Dechmann et al., 2009; Egert-Berg et al., 2018), seabirds follow the white plumage of foraging flocks (Beauchamp & Heeb, 2001) and penguins are able to capture more fish when foraging together (McInnes et al., 2017).

Foraging in groups can provide energetic benefits by increasing foraging success and by making energy intake more reliable (Giraldeau & Beauchamp, 1999; McInnes et al., 2017; Snijders et al., 2021). Individuals are required to maintain cohesion and spatiotemporal coordination to benefit from interactions with conspecifics (Conradt & Roper, 2005). While maintaining strong social bonds can provide long-term fitness benefits (Bohn et al., 2009; Silk et al., 2010), moving with group members can increase feeding competition and the immediate costs of transport (Usherwood et al., 2011). Less time and energy spent on finding food patches due to information provided by group members may be especially important for species foraging on ephemeral resources, but little evidence is available. The use of social information should decrease

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energy expenditure and/or increase foraging efficiency and result in higher rates of return during foraging bouts.

Bats are an excellent group to test how resource ephemerality and energy expenditure influence group foraging. They spend large proportions of their energy budget on locomotion that is fuelled by the food of the day (O'Mara et al., 2017) and feed on resources that are often widely dispersed and unpredictable. Bat species that forage for ephemeral insect swarms eavesdrop on the echolocation buzzes of other bats emitted during prey capture attempts (Dechmann et al., 2009, 2010; Egert-Berg et al., 2018). Beyond this often-opportunistic behaviour, some species will also search for food near group members to maximize the discovery of feeding patches (Dechmann et al., 2009, 2010; Egert-Berg et al., 2018). Bats of many species readily incorporate social information about food across a range of cues (O'Mara et al., 2014; Page & Ryan, 2006; Ramakers et al., 2016; Ratcliffe & ter Hofstede, 2005; Wright, 2016), and the nature of the resource they feed on as well as how tightly they depend on it can be used to predict whether and when social information should be used during foraging (Kohles et al., 2022).

Greater spear-nosed bats, *Phyllostomus hastatus*, seasonally feed on an ephemeral resource, the nectar of balsa trees, *Ochroma pyramidale*. In a well-studied population on Trinidad, female *P. hastatus* form stable life-long groups of unrelated females (McCracken & Bradbury, 1981; Wilkinson et al., 2016). They synchronize reproduction, converge on a loud group-specific call that requires extended learning and perform several cooperative behaviours at the group level, such as babysitting and pup guarding from infanticide attempts by neighbouring groups (Boughman, 1998; Boughman & Wilkinson, 1998; Wilkinson & Boughman, 1998; Wilkinson et al., 2016). They are omnivorous, but during the dry season, they feed nearly exclusively on balsa nectar. These pioneer trees are a rare and patchy resource, and the bats' group-specific social calls are hypothesized to recruit group members to flowering trees to exploit or defend them collectively (Wilkinson & Boughman, 1998). However, the number of flowers available on a given tree is limited (Kays et al., 2012), although many other animals feed on them, and the energy requirements of these bats are large (Kunz et al., 1998). Thus, the potential reasons for recruiting others to these flowers warrant further investigation, especially if *P. hastatus* social groups forage together to feed on these flowers. In addition, the availability of balsa and thus the value of social information (Kohles et al., 2022) may vary locally, and it is unclear whether group foraging and resource defence occur across this species' range.

We used high-frequency GPS loggers to tag three groups of *P. hastatus* in Panamá and recorded complete foraging trips. We used these GPS data to construct proximity-based social networks to test how social associations are linked with foraging performance and behaviour. We hypothesized that, like in Trinidad, *P. hastatus* forage in groups during the dry season. We thus expected them to commute to a food source socially (either as a group or as subgroups of individuals) and exploit it together. We also hypothesized that social foraging increases foraging success and that proximity that is within hearing distance of social calls increases foraging efficiency and lowers energy expenditure despite potential competition trade-offs. With this study we make an important contribution to how foraging behaviour may vary across sites and seasons, and thus, the intricate link between a local resource landscape and the resulting social behaviour.

METHODS

Data were derived from 39 adult *P. hastatus* (37 females, 2 males) that were captured from three roosting groups in a cave (‘La Gruta’) on Isla Colón, Bocas del Toro, Panamá using a bucket trap. Groups were captured sequentially and there was no overlap among groups on the nights they were tracked. Roosting groups were individuals co-roosting in small depressions on the cave ceiling, consistent with previous work in Trinidad. All bats from these groups were fitted with GPS tags, with the exception of two females that had heavily worn teeth and old, severe injuries. Both males were adult harem males, the females comprised 15 nulliparous young females and 19 postlactating females. GPS tag retrieval success varied among groups (group 1: 13 females and 1 male deployed, 5 females and 1 male (42.8%) recovered; group 2: 6 females deployed, 4 females (66.7%) recovered; group 3: 16 females and 1 male deployed, 8 females and 1 male (52.9%) recovered). Bats from a single social group were placed into a wire-mesh cage covered with a breathable cotton cloth where they roosted together calmly until removed for processing. We recorded mass to the nearest 0.5 g, measured forearm length to the nearest 0.1 mm and implanted each bat with a subcutaneous passive integrated transponder (PIT) tag (ID100; Euro ID, Frechen, Germany). To measure wing dimensions for flight power estimates, we took photos of one fully outstretched wing placed flat over 1 mm graph paper. Bats were fitted with a GPS data logger (Gypsy-5 GPS, TechnoSmart, Rome, Italy; O'Mara et al., 2021) that was wrapped in clear shrink tube. The logger was mounted on a silk collar (0.8 cm wide) and closed with Safil-C degradable suture (Aesculap/B. Braun, Co, Tuttlingen, Germany; O'Mara et al., 2014). The collar and GPS together weighed 6.8 ± 0.51 g, ~5.7 ± 0.4% of mean ± SE body mass (range 4.5–6.6%).

GPS tags were programmed to collect location fixes from 1800 to 0600 hours local time every 1–2 s. When there was not adequate GPS reception, tags went into a low energy sleep state for 5 min and then restarted to search for satellites for 90 s. Tag function varied due to the deep cave roost used by the bats and resting under presumably dense foliage while foraging. We retrieved 18 tags with analysable data: five females and one male from group 1, three females from group 2 and eight females and one male from group 3 (Appendix, Table A1). The 18 recovered tags collected 1–4 nights of data for a total of 34 bat-nights. We removed from analysis 5 nights from five different bats where fewer than 30 min were tracked for various reasons (e.g. the bat remained in the cave for most of the night draining the battery), leaving 29 bat-nights from 16 females and two males with a range of 75.5–307.5 min of data collected per night (mean ± SD: 197.31 ± 60.35; Appendix, Table A1). We tagged entire social groups and retrieved 42–67% of the tags per group. Inferences made reflect only social interactions reconstructed from these retrieved tags and not from the remainder of the social group, or from other social groups in the cave or from other caves in the surrounding area.

Decisions to forage with group members may rely on the overall energetic costs relative to feeding success of social foraging. We use airspeed to estimate instantaneous energy expenditure based on well-established flight power estimates (Pennycuick, 2008). To estimate flight airspeed and subsequent energy expenditure, wind data were collected at an automated weather station (9°21′4″N, 82°15′29″W) at 15 min intervals by the Physical Monitoring Program at the Smithsonian Tropical Research Institute for their Bocas del Toro field station and downloaded from http://biogeodb.stri.si.edu/physical_monitoring/research/bocas. Wind speed and direction were collected every 10 s with a RM Young Wind Monitor Model 05103. Mean wind speed and wind direction were then calculated at the end of every 15 min interval.

Ethical Note

This work was approved by the Ministerio del Ambiente, Panamá (SE/A-96-15) and the Animal Care and Use Committee at the

Smithsonian Tropical Research Institute (2014-0701-2017) and adhered to the ASAB/ABS Guidelines for the Use of Animals in Research. We attempted to minimize disturbance to the bats in the cave by only entering during captures and minimizing light exposure; however, this cave is frequently used by tourists, so we could not account for all disturbances to the bats. Handling of individual bats, including morphometric measurements, PIT tagging and attaching GPS collars was typically completed within 7 min and bats were then immediately released back into the cave.

Analysis

All analyses were conducted in R 4.2.1 (R Core Team, 2022).

Ground speed, wind speed and wind accommodation

We calculated ground speed (speed of movement relative to the ground) and bearing for successive time points in the 'move' package (Kranstauber et al., 2018). To calculate airspeed (speed of movement relative to the moving air column), we annotated wind speed and direction for each GPS location using a weighted interpolation of the U and V components of the available 15 min wind samples to match the higher resolution (0.5–1 Hz) of the GPS sampling (O'Mara et al., 2019; 2021; Safi et al., 2013). Wind support was calculated as the length of the wind vector in the direction of the bat's flight, where positive values represent tailwind and negative values headwind, and are given as total support in m/s. Crosswind was calculated as the absolute value of the speed of the wind vector perpendicular to the travel direction, and airspeed was calculated as the square root of ((ground speed wind support)^2 + crosswind^2).

Behavioural segmentation

To identify behavioural states of resting, slow foraging flight (i.e. feeding), moving between patches and commuting, we applied a four-state hidden Markov model in 'momentuHMM' (McClintock et al., 2018). These behaviours were chosen as they represent the most likely identifiable biologically meaningful behaviours derived from time series of GPS locations (de Weerd et al., 2015; Edelhoff et al., 2016; Gurarie et al., 2009, 2015). While the statistical identification of behavioural states is executed through a hidden Markov model (or machine learning or neural network), assignment to a particular behaviour of interest relies on recognizing the limitation of GPS data (time and location) and knowledge of how species move through an environment. Our four behavioural categories differed as follows: bats at 'rest' (i.e. no movement) accumulated substantial GPS error and there appeared to be erratic 'movement' in the data, with high step lengths (distances between GPS locations) at high turning angles (de Weerd et al., 2015). Slow 'foraging flight' had short step lengths with high turning angles, reflecting a slow searching flight pattern with short pauses. 'Move' was more directed flight between patches, with increasing step lengths and lower turning angles, and 'commute' included highly directed flight where bats were moving quickly with little deviation in their flight paths.

Behavioural states were entered into the hidden Markov model in order of increasing speed and decreasing turning angular mean (i.e. slow flight had larger turning angles, commuting flight was fast with high concentrated turning angles near zero), with step lengths modelled with a gamma error distribution and turning angles with a wrapped Cauchy distribution. Models were fitted for each bat on each bat-night, and each resulting model was visually inspected to ensure reasonable classification. The track for each bat-night was first regularized to 1 s intervals using a correlated random walk procedure in function 'momentuHMM::crawlWrap' and then passed to the hidden Markov model. We used simulations to target the number of identifiable states and identify the starting values for each state (McClintock et al., 2018; Michelot et al., 2017), and these simulations showed that the four-state model always performed better (had lower Akaike information criterion, AIC, values) than the three- or two-state models. On occasion, a five-state model had better fit although it was often difficult to discern biological meaning between the additional state that was placed very close to the low speed and higher turning angle behaviours of slow foraging flight.

We used a patch approach to identify foraging and resting (i.e. night roost) areas since aggregations of GPS locations should indicate a site of behavioural interest. For each bat-night, we defined a patch as a cluster of GPS locations that were classified as foraging (slow flight or moving) or as rest. These clusters were identified using density-based spatial clustering of applications with noise (DBSCAN) using function 'fpc::dbscan' (Hennig, 2020; Schubert et al., 2017) with a minimum of 15 points per cluster at a maximum spatial distance (eps) of 10 m among nearest neighbours. This distance was chosen through visual inspection of diagnostic plots in function 'dbscan::kNNdistplot' (Hahsler et al., 2019). To facilitate spatial comparisons across all individuals in the sequentially tracked groups, we labelled patches with centroids that were less than 30 m apart as a single patch regardless of the night on which they were used. This distance was chosen as there was a clear break in the distribution of pairwise distances among patch centroids and 30 m is slightly larger than the approximate diameter of a balsa crown. These patches were also ground-truthed to evaluate potential plant food composition and presence.

Once foraging patches were identified, we then further classified feeding locations that were likely flower clusters. We used the same DBSCAN procedure on the GPS locations within each foraging patch per bat-night to identify a flower cluster as a position with a minimum of six points per cluster within a maximum spatial distance of 0.8 m. This distance was chosen based on the spatial distribution of flowers observed within *O. pyramidale* (M. T. O'Mara & D. K. N. Dechmann, personal observations). We used these likely feeding clusters to define foraging efficiency as feeding clusters divided by the total time tracked (in min) per night.

Energy expenditure

The speed that an animal flies in an air column (airspeed) is the most important predictor of its mechanical power output and subsequent total metabolic power output. We estimated the mechanical power of flight in W (P_{mech}) following Pennycuick (2008) using calculated airspeeds, the capture mass of the animals and wing length taken from each bat's wing photo multiplied by two. An individual's average power curve was generated for each bat at the mean flight altitude (50 m) and 25 °C (Appendix, Fig. A1) and returned estimates across all individuals for the minimum power speed of 6.81 ± 0.21/ms and maximum range speed of 11.0 ± 0.35/ms. Minimum power speed represents the most efficient instantaneous flight speed and maximum range speed maximizes the range covered over ground per unit of energy expended. In general, bats should fly at their minimum power speed when moving short distances and at their maximum range speed when moving long distances (Hedenström, 2003). The airspeeds used by bats (7–9 m/s) were well within these estimates for energy-efficient flight. To estimate energy expenditure for each night, we calculated the instantaneous power output during flight for each GPS location at the observed altitude and airspeed. Mechanical power output alone underestimates metabolic power requirements (Pennycuick, 2008; von Busse et al., 2013; Ward et al., 2001). To estimate total metabolic power required, we estimated the metabolic power of flight (P_{met}) following Ward et al. (2001) using the mean estimated flight muscle partial efficiency (E_{FM}) for *P. hastatus* in a wind tunnel (0.24667, range 0.13–0.34; Thomas, 1975). Total metabolic power was then calculated as: $P_{met} = 1.1((P_{mech}/E_{FM}) + P_{BMR})$. For locations where the bat was at rest (including while in the cave), we substituted the resting metabolic rate (P_{BMR}) of 23.8 J/g per h (McNab, 1969) and converted this to 0.0661 W/g. These values were summed to daily energy expenditure (DEE) and compared to DEE values from smaller *P. hastatus* in Trinidad measured through doubly labelled water (Kunz et al., 1998).

To estimate energy returns from foraging, we used the energy content/ml of balsa nectar and the likely flower density/tree (Kays et al., 2012). Total nectar produced by a flower is estimated at 25.5 ml, and balsa nectar sugar concentration decreases over the night from 13.3% at 1800 hours to 7.9% at 0600 hours, with an average concentration of 12.4% total sugars (Kays et al., 2012). This is equivalent to 0.124 g of sucrose/ml nectar, yielding 0.47988 kcal/ml (3.87 kcal/g sugar × 0.124 g/ml). Balsa nectar then has an energy density of 2.007818 kJ/ml. Flowers open with a mean ± SD of 4.9 ± 1.3 ml of nectar, and there is a sharp decline in nectar production over the night. We assumed that bats drink the full nectar volume present when flowers open (5 ml), which likely overestimates the amount of nectar truly ingested during feeding events. Peak flower availability is approximately 60 flowers/patch or 5 flowers/m^2. However, the mean is 20 flowers/patch and 2.5 flowers/m^2, with flower density following a normal distribution over the season (Kays et al., 2012).

Social Proximity Effects on Behaviour

To test the effects of distance to a nearest neighbour on behaviour, we used the distance among individuals as a dynamic metric that could change with every second of tracking. We excluded commuting behaviour from this analysis after inspection of the data showed that individuals did not commute together with groupmates. We used this pairwise distance to further identify whether the changing proximity between individuals affects movement decisions. We limited the potential distance that behaviour could be affected by another individual to 290 m, which is the potential perceptual distance of *P. hastatus* social calls at a mean (± SD) peak call frequency of 6725 ± 36.3 Hz under ambient weather conditions (Stilz & Schnitzler, 2012). If social calls help coordinate movement behaviour, then bats within hearing distance of one another may be influenced by the movement and potential recruitment of group members.

We fitted generalized linear mixed effects models in ‘lme4’ with individual as a random intercept nested within social group (Bates et al., 2015). For models evaluating proportional activity budgets as a response, a binomial family was specified, and for all others, Gaussian models were used. When a nonlinear relationship seemed likely, we fitted second-order polynomial models and tested whether they fit the data more efficiently than a first-order model using the second-order Akaike's information criterion corrected for small samples (AICc) calculated using ‘MuMIn::AICc’. The most efficient model was the model with an AICc value at least three units lower than competing models. To evaluate the significance of the fixed effects, we calculated type II *P* values using Satterthwaite degrees of freedom method with ‘lmerTest::anova’ for Gaussian models (Kuznetsova et al., 2017) and with ‘car::Anova’ for binomial models. To measure the effect size of each Gaussian model, we calculated both the marginal R^2 (fixed effects, $R^2{}_m$) and the conditional R^2 (fixed and random effects, $R^2{}_c$) in ‘MuMIn’ (Bartoń, 2016).

RESULTS

Tracking Summary

The 18 tracked bats mostly foraged in sites that were 20–30 km away from their cave roost across the sea (Fig. 1), but one of the harem males foraged close to the cave and most individuals showed some indications of quick foraging stops on their return flights to the cave. We found no co-commuting flight within the 41 combinations of tagged pairs of bats. None of the tagged bats moved together to a foraging site in a way that would be consistent with social foraging. While GPS tags had the same programmed on/off time, because of low satellite coverage and late cave emergence, the first GPS record of each tag occurred a mean (± SD) of 149 ± 49 min after sunset. At this time bats were already commuting and were 5.2 ± 6.2 km from the roost when first locations were recorded (range 350–24.2 km). Each night, bats spent a mean (± SD) of 197 ± 60 min outside the roost and travelled a mean (± SD) of 59.2 ± 16.2 km (Appendix, Table A1). Bats commuted to their foraging areas with slight headwinds at a mean (± SD) ground speed of 8.63 ± 2.63 m/s (airspeed: 9.12 ± 2.69 m/s) and returned to the cave at a mean (± SD) ground speed of 7.89 ± 4.08 m/s (airspeed: 7.76 ± 3.82 m/s) flying with tailwinds, at airspeeds that were between their mean (± SD) minimum power speed (6.81 ± 0.21 m/s) and mean (± SD) maximum range speed (11.0 ± 0.35 m/s). Wind speeds were generally low during the tracking period, with prevailing offshore winds blowing eastward. Bats foraged at a mean (± SD) ground speed of 3.95 ± 3.43 m/s (airspeed: 4.15 ± 3.38 m/s).

Behaviour and Foraging Patch Use

We ground-truthed the foraging patches on the mainland and found flowering *O. pyramidale* trees in each of them. There were no flowering *O. pyramidale* on Isla Colón, but foraging patches always included flowering *Luehea seemannii*. It is unknown whether bats fed on the nectar of *L. seemannii* flowers, or on the animals attracted to this resource. All individuals completed the ca. 25 km commute from the roost to the foraging areas alone (Fig. 1c), with a mean ± (SD) distance of 9.1 ± 5.8 km from one another when commuting. Individuals then converged in the same foraging areas, mostly on the mainland. Individuals used a mix of slow flight, moving and resting during the approximately 200 min they were outside the cave, and this did not differ across the three groups (Fig. 2a). Bats spent a mean (± SD) of 24.0 ± 19.3% of their time in rest, 24.6 ± 14.6% of their time in slow foraging/feeding flights, 31.3 ± 23.6% of their time in faster foraging movements between feeding sites and 25.1 ± 16.8% of their time commuting. To examine social effects on foraging, we only further analysed behaviours other than commuting.

We identified 73 patches (dense clusters of GPS locations) that had 100% minimum convex polygon areas measuring a mean (± SD) of 4 ± 7 ha, which likely reflected large aggregations of feeding or roosting trees that were a mean (± SD) of 22.6 ± 31.6 km from the cave roost. Bats used a mean (± SD) of 7.2 ± 4.2 foraging patches (i.e. trees or groups of trees) per night, and patches were 4.0 ± 3.8 km apart. As bats increased their total nightly flight distance, they used more patches (estimate ± SD: 0.886 ± 0.034 per additional km, $F_{1,\ 20.174} = 6.861$, $P = 0.016$, $R^2{}_m = 0.13$, $R^2{}_c = 0.70$; Appendix, Fig. A2). Over the course of the night, bats used a mean (± SD) of 20.72 ± 19.91 feeding locations (flower clusters) (range 3–82). There was no relationship between the number of feeding locations they visited within the patches and the number of patches they used or the time they spent outside the roost (Appendix, Fig. A2).

While tagged bats did not commute together to the foraging sites, they would often occupy the same patches as other group members, and proximity to other tagged social group members influenced their behaviour. Bats were within hearing distance of one another (less than 290 m), and at the presumed threshold of social foraging influence a mean (± SD) of 0.11 ± 0.14% of each

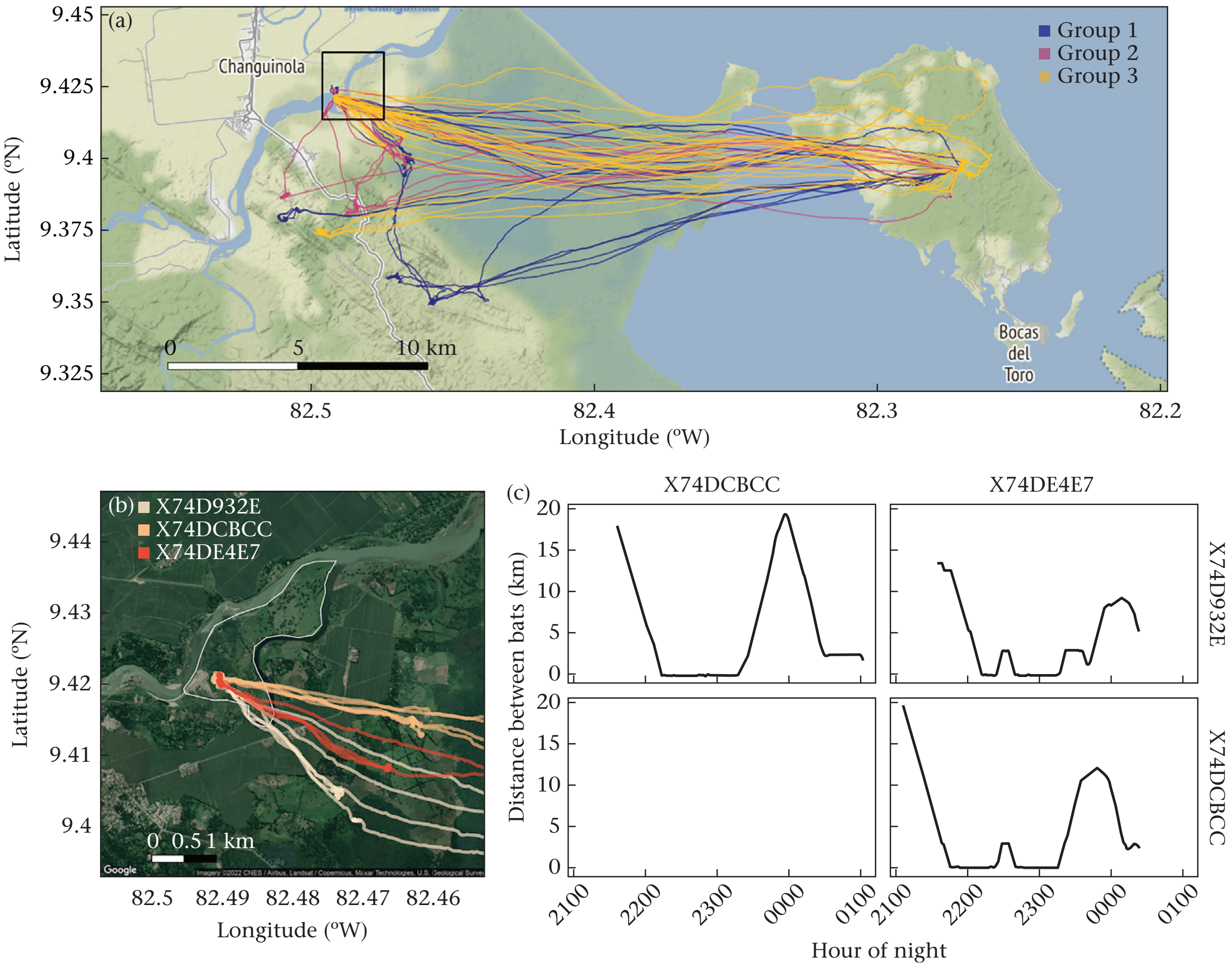

Figure 1. (a) Tracking overview with individuals coloured by group membership. (b) The island in the Changuinola river (Isla Changuinola) shown with three individuals from group 3 on 4 March 2016. (c) Pairwise distances between the three individuals in (b) across the same night. Note that in (c) both axes are repeated to show the simultaneous distance between pairs of individuals and the large distances among individuals at the beginning and end of the night when commuting. The tracked bats all used similar foraging areas far away from their cave, and no tagged bats commuted together to those sites. Instead, they reunited in the foraging patches 20–30 km from their home cave.

night's tracking (range 0–50.0%), and all of these locations occurred on Isla Changuinola for each of the three social groups (Fig. 2). Activity budgets differed depending on whether individuals were in the same patch as their neighbours or not (patch estimate: $F_{1,3} = 0.028$; Fig. 3a, b). When in the same patch, individuals were a mean (± SD) of 24.3 ± 21.4 m apart (0.25–133 m). The proportion of time spent in rest was larger when the nearest tagged bat was in the same patch as the focal individual, rather than when they occupied different patches that were within 290 m of one another (median ± MAD: same patch: 85.2 ± 18.6%; different patch: 32.2 ± 44.3%; $\chi^2_3 = 10.12$, $P = 0.018$; Fig. 3a). Bats varied in how much they synchronized behaviours with a nearest neighbour ($\chi^2_1 = 4.08$, $P = 0.043$; Fig. 3b). Nearest neighbours within a patch were more likely to synchronize resting than other behaviours (Fig. 3b). Bats rested a mean (± SD) of 19.3 ± 14.3 m away from their nearest tagged neighbour (range 0.47–25 km), and resting bouts were longer with decreasing distance from one another, especially within 3 m or less (power curve/Freundlich equation intercept ± SE = 2.95 ± 0.24 m, $P < 0.001$; Fig. 4).

Despite groups being tracked on different nights, the same resting areas tended to be used by bats across all social groups, regardless of the tracking night. We identified 43 resting areas, and one of these resting locations on Isla Changuinola was used by 11 bats over 5 nights (Appendix, Fig. A3). Three other locations on Isla Colón were used repeatedly by a single bat over 2 nights. The remaining 39 sites were used by one bat on 1 night each.

Energy Costs and Feeding Requirements

Estimated mean (± SD) daily energy expenditure (DEE) was 198.47 ± 69.44 kJ/day and increased with tracking time (estimate ± SD: 0.729 ± 0.174, $F_{1,25.61} = 17.462$, $P < 0.001$, $R^2_m = 0.383$, $R^2_c = 0.448$; Fig. 5a). This is similar to DEE estimates based on allometric estimates from body mass alone of 153.02 ± 5.96 kJ/day (range 143.07–164.89 kJ/day; Speakman, 2005) and to DEE derived from doubly labelled water measurements in *P. hastatus* that were 36% smaller than those at our study site (mean ± SD: 76.8 ± 6.6 g versus 121.5 ± 7.6 g in this study; estimates from Kunz et al. (1998) are shown in blue in Fig. 5a).

The proportion of time spent less than 290 m from other individuals did not predict total daily energy expenditure ($\chi^2_1 = 2.07$, $P = 0.15$) or the number of feeding clusters visited by individuals ($\chi^2_1 = 0.30$, $P = 0.58$). We converted the estimated energetic needs for each individual into the number of full *O. pyramidale* flowers required to support them. We found that individuals fed from an increasing number of flower clusters as their total estimated energy needs increased (second-order polynomial estimate ± SD = 55.45 ± 14.89, 27.73 ± 14.86,

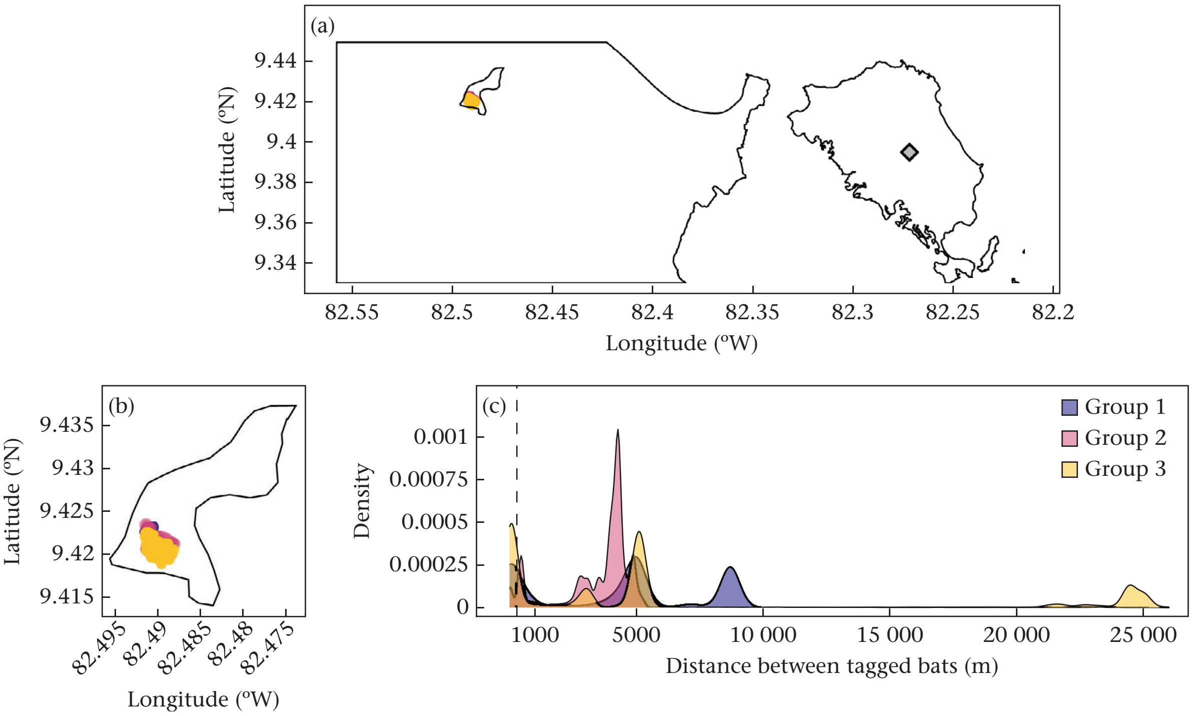

Figure 2. Distances between tagged bats, including the GPS locations that were within the hearing threshold of another tagged group member and the assumed threshold for social interaction (290 m), for (a) the study area and (b) Isla Changuinola. (c) Total density distributions for all pairwise distances. The capture site is noted with a diamond on Isla Colón in (a). All locations within this threshold were found on Isla Changuinola for each of the three study groups. The vertical dashed line in (c) denotes the 290 m transmission threshold of *P. hastatus* social calls.

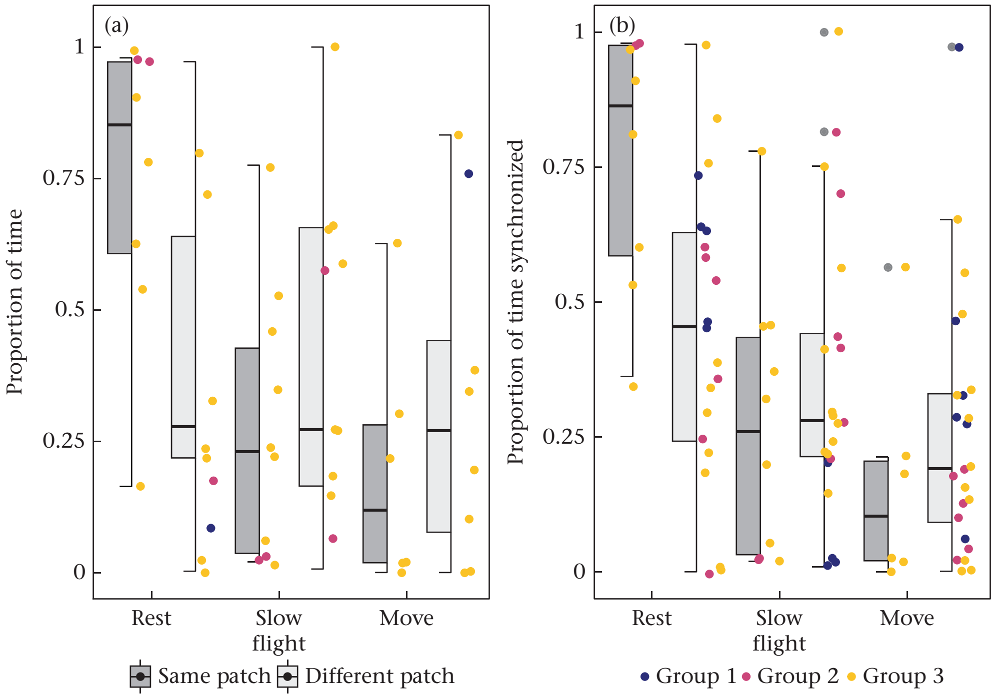

Figure 3. (a) Bat nightly activity budgets when the nearest neighbours occupied the same and different patches but were within 290 m of one another. (b) Behavioural synchrony of nearest neighbours in and out of the same patch. Box plots show the proportion of time engaged in behaviours for each patch category, and points show the proportions for each individual bat per night.

$F_{2,26.45} = 8.84$, $P = 0.001$, $R^2_{m} = 0.376$, $R^2_{c} = 0.494$; Fig. 5b). Estimated energy expenditure, as measured through movement, more strongly depended on the total time tracked per night than on the proximity relationships among individuals in a social group, and these closer foraging distances did not predict foraging efficiency.

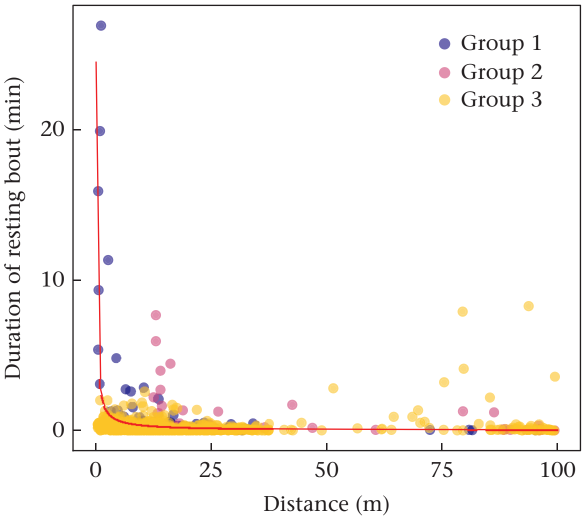

Figure 4. Duration of continuous resting bouts relative to the distance to a bat's nearest neighbour.

DISCUSSION

Based on previous work (Wilkinson & Boughman, 1998), we predicted that *P. hastatus* would commute to foraging patches together and forage with their social group to feed on *O. pyramidale* flowers. Instead, we did not find any tagged individuals commuting together to the foraging patches. They commuted over long distances that included the ocean and large commercial banana plantations, landscapes that have few available resources to these bats. Tracked individuals then used the same foraging patches, but on different feeding locations within the patch. When individuals were near group members, they tended to rest, and resting bout duration increased with closer proximity to others. Closer distance between individuals did not decrease daily energy expenditure or increase foraging success. It appears that while a driving benefit of social foraging is often assumed to be increased foraging success (Giraldeau & Beauchamp, 1999; McInnes et al., 2017; Snijders et al., 2021), this did not seem to be the case under the resource conditions during our tracking study. Instead, resting in *P. hastatus* groups may reinforce social bonds or has benefits outside of foraging efficiency such as predator detection.

Social foraging should increase foraging efficiency, either because food patches are detected more efficiently or because of social facilitation increasing feeding rates. With increasing group size, Trinidad guppies, *Poecilia reticulata*, decrease the time it takes to locate food patches and increase their intake rates (Snijders et al., 2021). Larger guppy groups act as more efficient sensors, but this comes at a cost of perceived feeding competition that drives increased bite rates. Individuals of many bat species forage socially to eavesdrop on feeding calls when resources are ephemeral and searching costs are high (Egert-Berg et al., 2018; Fenton, 2003), and some species show extraordinarily coordinated group foraging for these ephemeral resources (Dechmann et al., 2009, 2010; Kohles et al., 2022). We found no effect of proximity between group members on time spent foraging, the number of foraging patches or the number of feeding locations.

Astonishingly, we found that individual *P. hastatus* from multiple social groups used the same patches of *O. pyramidale*, but that they commuted over 25 km from their roost without other tagged group members. *Phyllostomus hastatus* in Trinidad were previously found to forage within 10 km of their roost (McCracken & Bradbury, 1981; Williams & Williams, 1970). Displacement studies showed that most *P. hastatus* individuals successfully navigated back to their home roost after displacement of up to 20 km. At 30 km or more, bats often failed completely to return home (Williams & Williams, 1970). This indicates that the distance at which our study animals were foraging from their cave was at the edge or even outside the range they were familiar with. They had to cross the sea and large commercial banana farms to reach the *O. pyramidale* foraging locations on the mainland. During our resource ground-truthing we found that on their home island and elsewhere south and east on the mainland *O. pyramidale* was not yet available. This suggests that once an isolated *O. pyramidale* patch is discovered, especially early in the flowering season, social information about this quickly moves through a colony. Once they

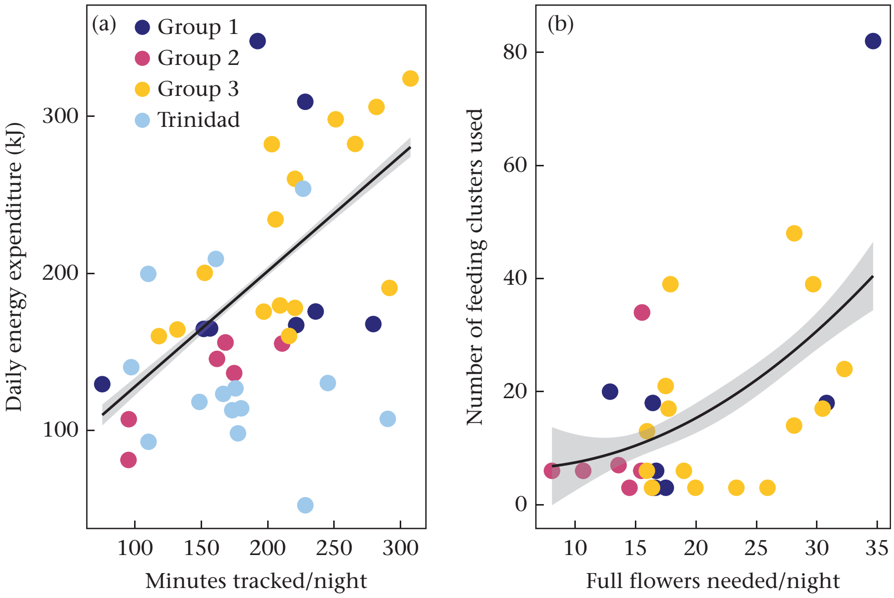

Figure 5. (a) Estimated daily energy expenditure and minutes tracked/night for groups 1–3 in the present study, with comparative data from smaller *P. hastatus* in Trinidad (from Kunz et al., 1998). The line shows the relationship derived from the individuals tracked in the present study. (b) Relation between the number of feeding clusters used/night and the number of flowers needed to support the energy requirements of an individual's estimated energy expenditure, based on average energy content/flower.

have located it, group members commute to the patch alone. *Phyllostomus hastatus* feeds on various food sources throughout most of the year, but almost exclusively switches to *O. pyramidale* when it is available during the dry season (Wilkinson & Boughman, 1998). It is unknown whether this is due to a shortage of other food sources, or to a distinct preference for nectar. However, to locate this widely distributed food source, bats may rely on social information transfer (Kohles et al., 2022). This may be a rare, but crucial, resource during the transition period when few trees are flowering and finding food is more unpredictable. Further tracking, mapping of the resource landscape and detailed dietary analysis are needed to identify how and when bats switch between food resources and the behavioural and energetic correlates of this change.

While they commuted without other tagged individuals, we found that some bats reunited with social group members in these patches, while others tended to forage completely on their own. This is similar to vampire bats, *Desmodus rotundus*, that fly individually to cattle approximately 300 m away where they then feed with partners with whom they have close social relationships (Ripperger & Carter, 2021). Previous radiotracking of *P. hastatus* in Trinidad found that during most of the year, social group members foraged alone and did not depart from or arrive at the cave together, but on rare occasions they joined a groupmate in a nearby foraging area (McCracken & Bradbury, 1981). Members of social groups occupied adjacent foraging ranges and social groups were segregated across the landscape (McCracken & Bradbury, 1981), unlike the large overlap we found during this study. Groups in Trinidad were more likely to depart together, and females from the same social group were captured around an *O. pyramidale* feeding site more often than randomly expected during the dry season (Wilkinson & Boughman, 1998). There also appears to be strong social attraction among Trinidad *P. hastatus* groups. Social calls broadcast at flowering *O. pyramidale* attracted bats, and social calls from flying *P. hastatus* were most often noted 3–4 h after sunset during foraging (Wilkinson & Boughman, 1998). The higher spatial and temporal resolution of our GPS tracking now indicates that *P. hastatus* are not only attracted to the possibility of food resources, but that they may form resting associations while outside their roost. These resting areas appeared to be conserved across our sequentially tracked social groups and could indicate that bats from the caves on Isla Colón tend to rest in larger aggregations during foraging. This may keep groups together, but also could have strong antipredator benefits. Further work targeting these foraging and resting sites through acoustics or thermal tracking would give further insight into the behaviour of these groups away from their roosts.

There could be regional or population differences in the main drivers on social group formations depending on the resource landscape. In Trinidad, it has been hypothesized that recruitment of group members to flowering trees may predominantly help bats defend trees against competitors (Wilkinson & Boughman, 1998). In Panamá, however, large animals that bats cannot defend against, such as kinkajous and opossums are the main visitors of *O. pyramidale* flowers (Kays et al., 2012). A flowering *O. pyramidale* with mean peak flower availability of 60 flowers/night provides approximately 600 kJ of energy at the beginning of the night. This is before nectar pools are depleted and trees begin producing less energy-dense nectar (Kays et al., 2012). We estimated that our tracked bats expended 198 ± 69 kJ/day, indicating that a single *O. pyramidale* crown could support the daily energy needs of only three to seven bats. Such a limited resource may be worth defending from conspecifics if all available flowers could be fully exploited (Wilkinson & Boughman, 1998), but a single tree would not support the needs of an entire social group of bats, and large clusters of trees would be needed to supply a social group's daily energy needs. This suggests that a collective resource defence is not the likely explanation for foraging near groupmates for this population in Panamá.

While foraging success did not appear to rely on social foraging during our tracking study, there are other highly relevant reasons for individuals in a social group to associate with one another. Within social groups that are structured at least partly by kin relationship, strong social bonds between related individuals have numerous life history advantages (Silk, 2007), extending life spans (Barocas et al., 2011; Silk et al., 2010), success in group conflicts (Samuni et al., 2021) and individual reproductive success (Frere et al., 2010; Schülke et al., 2010; Silk et al., 2003). On Trinidad, however, female *P. hastatus* form stable, relatively closed groups of unrelated females that stay together for their lifetime and show highly developed social bonds (McCracken & Bradbury, 1981; Wilkinson et al., 2016). They develop group-specific social calls (Boughman, 1997; Wilkinson & Boughman, 1998) and recognize and guard group members' offspring (Bohn et al., 2007, 2009). Low reproductive rates and high infant mortality in this species (Stern & Kunz, 1998) are strong selective pressures on potential cooperation among unrelated females. The ecological and physiological conditions structuring *P. hastatus* social groups may be similar to groups of unrelated females in wild equids (Cameron et al., 2009) and some cooperative breeding birds (Riehl & Strong, 2018). The exact purpose of this close resting behaviour while foraging and whether this is a common phenomenon or a result of exceptional circumstances in this season and population remain unknown and warrant further study.

Social information may mainly be used for the discovery of feeding areas. Commuting to repeatedly used foraging patches 25 km or more from a central roost may not be unusual for some bats (Calderón-Capote et al., 2020; Goldshtein et al., 2020; Harten et al., 2020; O'Mara et al., 2021), but still presents navigational and energetic risks due to the long distances travelled and potential weather hazards. Nectar- and fruit-feeding fruit bats appear to have large and robust cognitive maps of their foraging ranges (Harten et al., 2020; Toledo et al., 2020). These species all commute from a common roost to distant foraging patches, but there is little to no overlap among individual foraging ranges in animals from these roosting aggregations, and these nonoverlapping ranges may be developed through reinforcement learning that minimizes competition (Goldshtein et al., 2020).

Further work mapping resources as seasons change and social groups reach decision points to alter their movements will help elucidate the intricate relationship between social behaviour and foraging behaviour and its energetic context. There may be strong variation among populations that differ in the resource landscapes they encounter but it may allow us to better understand the links between species' ecological niches and how sociality responds to resource environments and the need for information use.

Author Contributions

M. Teague O'Mara: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing – original draft; Writing – review & editing. **Dina K. N. Dechmann**: Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Validation; Writing – original draft; Writing – review & editing.

Declaration of Interest

None.

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Appendix

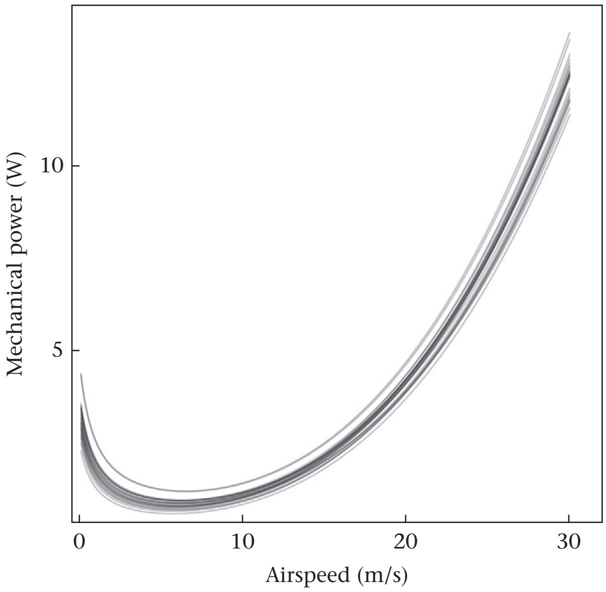

Figure A1. Mechanical power requirements at airspeeds for each bat in this study. Power output was calculated following Pennycuick (2008) at 50 m and 25 °C using each individual's body mass and wing dimensions.

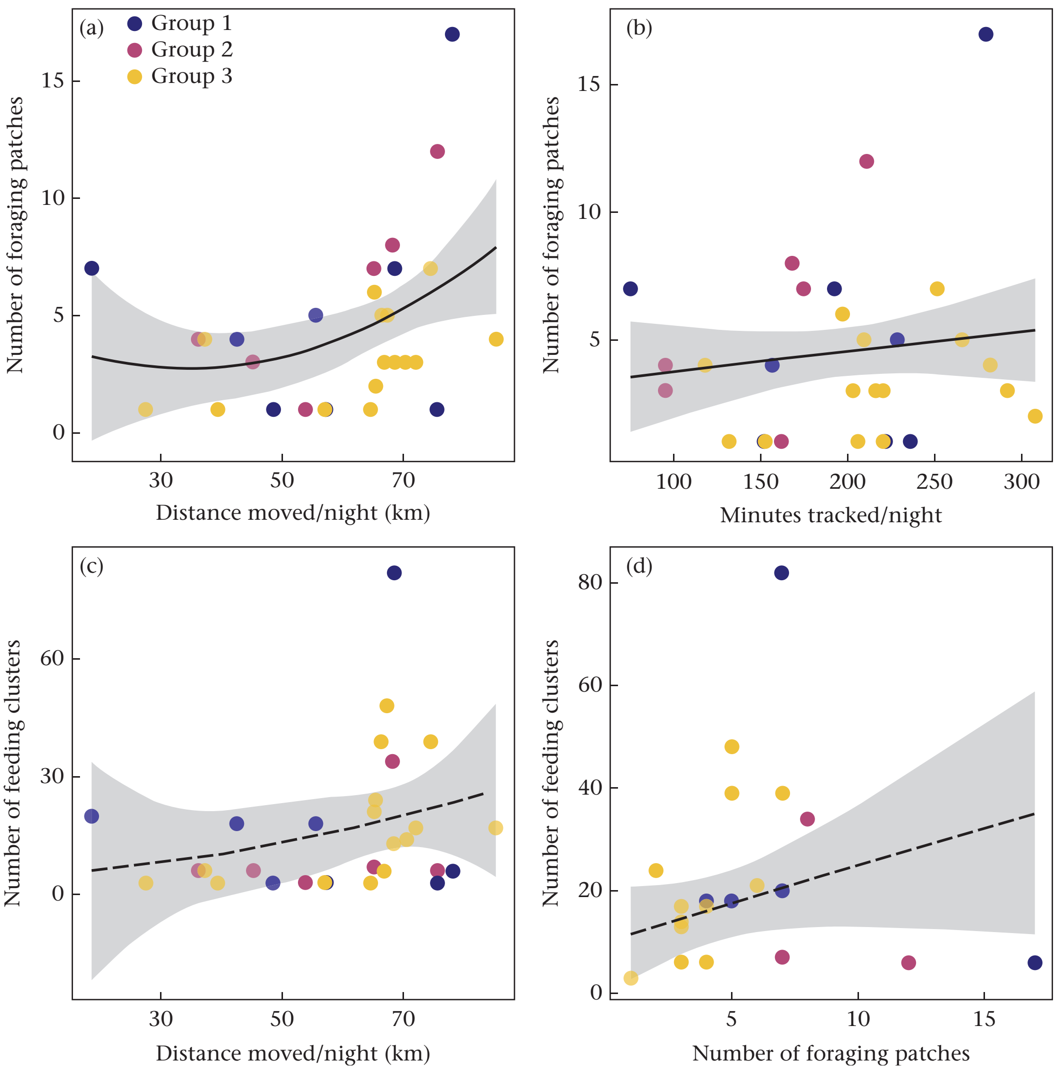

Figure A2. Individual nightly summaries for foraging and feeding. The number of foraging patches used in relation to (a) the distance that individuals moved each night and (b) the total time that individuals were tracked each night. The number of feeding clusters identified in relation to (c) the distance moved per night and (d) the number of foraging patches used. Statistically significant slopes that differed from zero are shown by solid lines, nonsignificant slopes are shown by dashed lines and shaded areas indicate 95% confidence intervals.

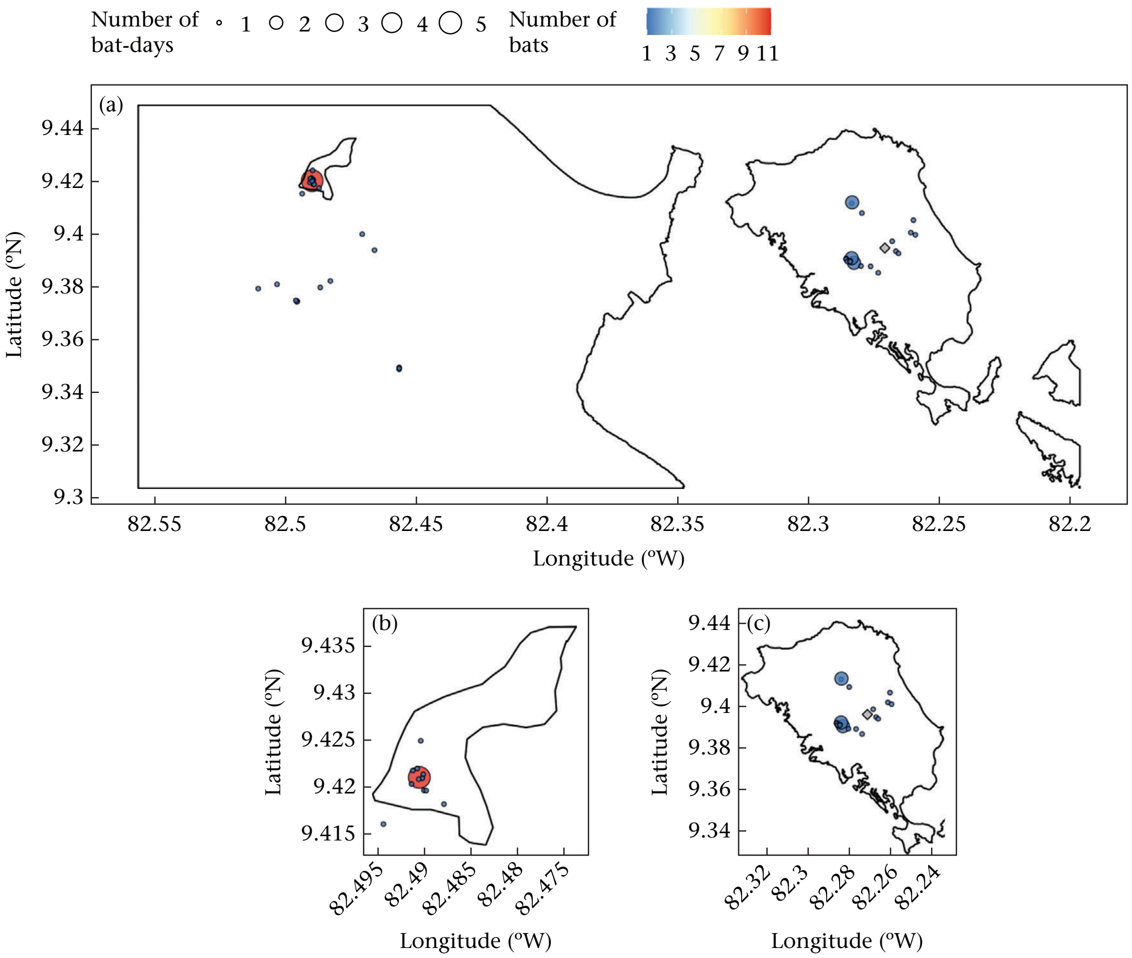

Figure A3. Resting patches clustered from GPS locations across (a) the study area, (b) Isla Changuinola and (c) Isla Colón, scaled by the number of individual bat-days that the sites were used and coloured by the number of individual bats that used each patch.

Table A1

Biometric and tracking information for the individuals analysed in this study

Bat ID	Group	Sex	Reproductive state	Mass (g)	Forearm length (mm)	Wing length (mm)	Wing area (mm^2)	Nights analysed	Time analysed (min)	Number of locations used	Distance tracked (km)
2016030703	1	M	Nr	134	93.5	271.96	22966.52	2	133.99±82.68	7296.5±3939.29	43.61±35.34
2016030705	1	F	Plac	124	87.8	280.82	24543.47	1	156.67	7694	42.55
71A0D95	1	F	Nulli	122	89.9	282.74	24088.56	2	224.89±4.82	12371.5±1289.06	56.38±1.2
71A111A	1	F	Nulli	109	90.8	296.86	25587.39	1	279.52	16752	78.12
74DDA80	1	F	Nulli	123	91.2	278.44	23724.58	1	151.88	6268	48.52
74DE9A7	1	F	Plac	122	91.5	274.95	23752.23	1	236.13	13488	65.24
74D8954	2	F	Plac	128	93.02	317.17	29422.44	1	161.88	6211	53.89
74DA92F	2	F	Plac	109	87.6	250.07	19667.46	2	192.87±25.53	6767±1236.02	70.42±7.41
74DCA83	2	F	Nulli	123	92.1	300.31	29703.42	2	131.85±51.45	5028±2224.56	56.72±16.26
74D8C25	3	F	Nulli	131	93.2	308.25	28074.65	1	118.15	5158	37.24
74D932E	3	F	Nulli	116	93.6	304.29	28397.6	2	207.63±2.4	8783±83.44	61.74±6.62
74DAF9C	3	F	Nulli	126	94.5	296.29	26317.99	1	95.27	5628	36.18
74DCBCC	3	F	Plac	114	89.7	289.26	22936.64	2	278.75±18.27	11910±1578.26	67.05
74DE4E7	3	F	Plac	124	94.2	296.11	26383.96	1	197.03	6618	65.24
74F7D4C	3	M	Nr	137	93.2	277.12	23586.97	1	152.63	3748	27.52
74F8E19	3	F	Plac	113	91.7	289.38	25321.02	3	201.26±61.87	7702.67±2597.55	62.01±19.62
74F9F83	3	F	Plac	116	92	284.51	24720.16	3	264.17±54.4	7866.33±1690.4	76.79±10.33
74FE24E	3	F	Plac	113	91.7	270.5	22057.56	2	218.35±3.15	7528±622.25	66.52±2.7

Nr: nonreproductive; Plac: postlactation; Nulli: nulliparous. Means (± SD) are given for nightly values for the minutes of tracking and the number of locations used when more than one night was recorded.