Lay Summary

Social foraging can increase foraging efficiency on hard-to-find food sources. Miniaturized high-frequency GPS allowed us to test this on groups of greater spear-nosed bats. We estimated food intake rates, energy expenditure, and the strength of bat social relationships. In contrast to our expectations, we did not find a relationship between bat social relationships and energy expenditure or foraging efficiency. However, bats took longer resting breaks when group members were close. Why these bats commute 25 km individually across the ocean to then forage near each other thus requires further investigation.

Greater spear nosed bats in Panamá do not use social proximity to improve foraging efficiency

Abstract

Group foraging animals may change their spatial relationships in response to the resource landscape. The strength of social network ties across foraging groups could then reflect the energy balance of individual group members through their effect on foraging efficiency. Greater spear-nosed bats (*Phyllostomus hastatus*) live in social groups where unrelated females develop group-specific social calls, defend each other's offspring, and are hypothesized to coordinate social foraging to feed on balsa flowers. To test if social groups forage together, and if this increases foraging efficiency, we tracked 18 individuals from three social groups of *P. hastatus* on Isla Colón, Panamá using high frequency GPS for 1 – 3 days each. We found that individuals commuted alone but then joined group members in small foraging patches with high densities of flowering balsas, 25 km from their roost on the mainland. Proximity-based social network measures did not predict foraging efficiency or energy expenditure, but individuals with higher social associations spent more time outside of the cave. Individuals did not coordinate movement, but close proximity among individuals increased resting bout duration and synchrony, particularly when in the same patch. These results show that stronger social proximity associations were more closely

tied to resting behavior, and indicate that factors other than increased feeding efficiency may structure network relationships of group members while foraging.

Keywords: GPS tracking, movement ecology, energy expenditure, foraging, social behavior

Introduction

Animals must respond to changes in the spatiotemporal distribution of resources, and their movement decisions to search for and exploit food resources directly impacts the ability to satisfy dietary requirements and affects 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 and Vicsek, 2014; Valone, 1989). For example, fish track moving refugia by matching speed to group mates (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 and Heeb, 2001), and penguins are able to capture more fish when foraging together (McInnes et al., 2017).

Foraging in groups can convey energetic benefits by increasing foraging success and make energy intake more (Giraldeau and Beauchamp, 1999; McInnes et al., 2017; Snijders et al., 2021). To benefit from interactions with conspecifics, individuals are required to maintain a degree of cohesion and spatial and temporal coordination in their activities (Conradt and Roper, 2005). While maintaining strong social bonds can provide long-term fitness benefits (Bohn et al., 2009; Silk et al., 2003), moving with group members can increase immediate costs of transport, and feeding competition. However, few studies have directly addressed the energetic trade-offs of social foraging or changes in the variance in food intake (Snijders et al., 2021). 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.

Bats are an excellent group to test how resource ephemerality directs group foraging. They spend large proportions of their energy budget on locomotion that is fueled 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 that reveal where an individual is attempting to capture (Dechmann et al., 2009; Egert-Berg et al., 2018; Fenton, 2003). Beyond this potentially opportunistic attraction to a resource, social group members of some species will also forage near each other to maximize the discovery of these feeding patches (Dechmann et al., 2009; Dechmann et al., 2010). Bats of many species readily incorporate social information about food across a range of cues and modalities (O'Mara et al., 2014a; Page and Ryan, 2006; Ramakers et al., 2016; Ratcliffe and ter Hofstede, 2005; Wright, 2016) reinforcing the inherently social nature of their foraging ecology.

To test the potential energetic benefits of foraging together, we tracked social groups of greater spear-nosed bats (*Phyllostomus hastatus*) in Panamá. Due to bat nocturnal lifestyles, acoustic cues are necessary for the coordination of group movement, and since sound has a relatively short transmission distance, bat social groups should move close to one another in a coordinated fashion. In a well-studied population on Trinidad, female *P. hastatus* form stable closed groups of unrelated females that stay together for their lifetime (McCracken and Bradbury, 1981; Wilkinson et al., 2016). Females in these social groups synchronize their reproduction, converge on a group-specific call that requires extended learning, and perform several cooperative behaviors at the group level, such as babysitting and pup guarding from the infanticide attempts of neighboring groups (Boughman and Wilkinson, 1998; Boughman, 1998; Boughman, 2006; Wilkinson and Boughman, 1998; Wilkinson et al., 2016). These omnivorous bats have diverse diets, but during the dry season, they feed nearly exclusively on the nectar of balsa trees (*Ochroma pyramidale*).

These pioneer trees are a rare and patchy resource and females are hypothesized to use group-specific social calls to recruit group members to flowering trees and exploit or defend them collectively (Wilkinson and Boughman, 1998). However, the number of flowers available on these trees is limited at any given time (Kays et al., 2012), and the energy requirements of these bats are large (Kunz et al., 1998) which may increase competition. In addition, the availability of balsa may vary locally and it is unclear if group foraging and resource defense occurs across the species' range.

We used high frequency GPS loggers to track 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 influence foraging performance and behavior. Based on the previous literature we hypothesized that (H1) *P. hastatus* forage in groups during the dry season and (H2) group foraging increases foraging efficiency despite competition trade-offs. We predicted that (P1) individuals with stronger proximity networks forage in the same food patches, and (P2) network strength centrality is positively associated with foraging efficiency and negatively associated with nightly energy expenditure. However, we found no clear evidence for social foraging or on energy expenditure. *Phyllostomus hastatus* at our study site in Panamá seem to behave profoundly differently from what was described previously.

Methods

We analyzed data of females from three social groups: five females and one male from group one, three females from group two, and eight females and one male from group three (Table S1). The 18 bats collected one to three nights of data, and we analyzed 30 complete bat nights (with a range of 75.5 – 307.5 min of data collected per night (mean ± sd: 197.31 ± 60.35). Groups were captured and tracked sequentially, with no overlap in tracking among groups.

These data were derived from 40 adult *Phyllostomus hastatus* (38 F / 2 M) that were captured from three social groups in a cave ("La Gruta") on Isla Colón, Bocas del Toro, Panamá using a bucket trap. Social groups were defined as individuals co-roosting in small depressions on the cave ceiling, consistent with previous work in Trinidad. Both males were adult harem males, and the females comprised 15 nulliparous young females, and 19 postlactating females. 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. Bat mass was recorded to the nearest 0.5 g, forearm length measured to the nearest 0.1 mm, and each bat received a subcutaneous PIT tag (ID100; Euro ID, Frechen, Germany). To measure wing dimensions for flight power estimates, wing photos were taken of one fully outstretched wing placed flat over mm graph paper. A subset of bats from each group were fitted with a GPS data logger (37 tags, 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., 2014b)). Total collar + GPS weight was 6.8 ± 0.51 g, which represented 5.7 ± 0.4 % of body mass (range: 4.5 - 6.6 %).

GPS tags were programmed to collect location fixes from 18 h – 06 h local time at 0.5 or 1 Hz. When adequate GPS reception was not received, tags went into a low energy sleep state for five minutes and then restarted to search for satellites for 90 seconds. The GPS tags had variable functionality due to both the deep cave roost used by the bats and roosting under presumably dense foliage while foraging. The 18 recovered tags collected one to four nights of data for a total of 34 bat nights. We removed from analysis five nights of tracking from five different bats that were less than 30 mins for various reasons (e.g., the bat remained in the cave for most of the night draining the battery), leaving 30 bat nights from 16 females and 2 males.

Wind data were collected at an automated weather station (9.351, -82.258) 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 seconds with a RM Young Wind Monitor Model 05103. Mean wind speed and wind direction were then calculated at the end of every 15-minute interval.

Analysis

All analyses were conducted in R 4.02 (R Core Team, 2020).

Ground speed, wind speed, and wind accommodation.

Ground speed (speed of movement relative to the ground) and bearing were calculated for successive time points in the *move* package (Kranstauber et al., 2012). To calculate airspeed (speed of movement relative to the moving air column) wind support and crosswind for were annotated for each GPS location using a weighted interpolation of the U and V components of wind to match the resolution of the GPS sampling (O'Mara et al., 2021; O'Mara et al., 2019; 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 ms^{-1}. 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].

Behavioral segmentation

To identify behavioral states of resting, slow foraging flight (or feeding), moving between patches, and commuting, we applied a four state hidden Markov model in *momentuHMM* (McClintock et al., 2018). These behaviors were entered into the 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 modeled with a gamma error distribution and turning angles with a wrapped Cauchy distribution. Models were fit 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 regularized to one-second 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 four state model always performed better (had lower AIC values) than 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 behaviors of roosting and slow foraging flight.

We used a patch approach to identify foraging and resting (night roost) areas since aggregations of GPS locations should indicate a site of behavioral interest. For each bat night a patch was defined 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 neighbors. 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 labeled patches with centroids that were less than 30 m apart as a single patch regardless of the night on which it was 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 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. pyrimidale*. We used these likely feeding clusters to define foraging efficiency as feeding clusters divided by the total time tracked (in minutes) 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. We estimated the mechanical power of flight in Watts (P_{mech}) following Pennycuick (2008) using calculated airspeeds, the capture mass of the animals, and wing length taken from a photo of the bat's fully outstretched wing over graph paper multiplied by two. An individual's average power curve was generated for each bat at the mean flight altitude (50 m) and 25°C (Figure S1) and returned estimates across all individuals for the minimum power speed of 6.81 ± 0.21 m s^{-1} and maximum range speed of 11.0 ± 0.35 m s^{-1}. Minimum power speed represents the most efficient instantaneous flight speed and maximum range speed maximizes the range covered over ground per unit energy expended. In general, bats should fly at their minimum power speed when moving short distances and at the maximum range speed when moving long distances (Hedenström, 2003). To estimate energy expenditure for each night, the instantaneous power output during flight was calculated 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^{-1} h^{-1} (McNab, 1969) and converted this to 0.0661 W g^{-1}. These values were summed to daily energy expenditure (DEE) and compared to DEE values from smaller *P. hastatus* in Trinidad measured through doubly labeled water (Kunz et al., 1998).

To estimate energetic returns from foraging, we used the energy content per ml of balsa nectar and the likely flower density per 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 18 h to 7.9 % at 06 h, with an average concentration of 12.4% total sugars. This is 0.124 g sucrose per ml nectar that yields 0.47988 kcal per ml (3.87 kcal/g sugar *0.124 g ml^{-1}). Balsa nectar then has an energy density of 2.007818 kJ ml^{-1}. Flowers open with 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). Peak flower availability is approximately 60 flowers per patch or 5 flowers per m^2. However, the mean is 20 flowers per patch and 2.5 flowers per m^2, with flower density following a normal distribution over the season.

Social Proximity Effects on Behavior

To test the effects of distance to a nearest neighbor on behavior we used the distance among individuals as a dynamic metric that could change with every second of tracking. We also used this distance and if the focal individual's nearest neighbor was in the same patch to further identify if the changing proximity between individuals affects movement decisions. We limited the potential distance that behavior could be affected by another

individual to 500 m, which is twice the potential perceptual distance of *P. hastatus* calls at a peak call frequency of 6725 ± 36.3 Hz at ambient weather conditions (Stilz and Schnitzler, 2012).

To test if cumulative proximity relationships influence behavior, we constructed individual-level proximity-based social networks across all tracking nights in *spatsoc* (Robitaille et al., 2019). GPS fixes were grouped to one-minute intervals, and proximity was assessed as a binary variable at a distance threshold of less than 30 m. This is twice the spatial error of a stationary tag (14.22 ± 12.05 m (O'Mara et al., 2021)), although error decreases dramatically when in flight (Ranacher et al., 2016), and is slightly larger than the approximate diameter of a balsa crown. We then calculated single values for strength centrality and degree for each individuals in *asnipe* (Farine, 2013), with edge weights as a simple ratio index of individuals within 30 m of each other. We used strength centrality of each individual in subsequent analyses as it reflects how much the focal bat was within 30 m of other individuals (Wyman et al., 2021), as well as degree (the number of different individuals that came within 30 m, Supplemental Table 1). We also wanted to identify if there were particular spatial locations that were used by bats across the social groups since groups were tracked sequentially and did not overlap in time. To do so we created an undirected patch use network with edge weights as the simple ratio index of the presence or absence of the use of a foraging patch by an individual. We used fast-greedy community detection in *igraph* to identify if there were foraging patches that were commonly used among individuals from multiple social groups at different times (Clauset et al., 2004). These communities then show how spatial location can connect individuals and groups across time.

Generalized linear mixed effects models were fit in *lme4* with individual as a random intercept nested within group (Bates et al., 2015). For models evaluating on proportional activity budgets as a response, a binomial family was specified and for all others Gaussian

models were used. When a non-linear relationship seemed likely, we fit second order polynomial models and tested if they fit the data more efficiently than a first order model using the second-order Akaike Information Criterion calculated using *MuMIn::AICc.* The most efficient model was the model with an AICc value at least 3 units lower than competing models. To evaluate the significance of the fixed effects in the models, 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, R^2 was calculated for both the marginal (fixed effects, R^2_m) and conditional (fixed and random effects, R^2_c) in *MuMIn* (Bartoń, 2016). The full GPS data set and code are available from the Movebank Data Repository (doi released on acceptance, code and data with environmental and behavioral annotation is available at Dryad for review: https://datadryad.org/stash/share/DBJdu_DVmEVBp6Yeq5x2RwupCy6W9NOaprjDtUZIH3E or at https://github.com/teague0/hastatusForaging).

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). 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 was 149 ± 49 min after sunset. At this time bats were already commuting and 5.2 ± 6.2 km from the roost when first locations were recorded (range: 350 m – 24.2 km). Each night, bats spent 197 ± 60 minutes outside the roost and traveled 59.2 ± 16.2 km. Bats commuted to their foraging areas with slight headwinds at ground speeds of 8.63 ± 2.63 m s^{-1} (airspeed: 9.12 ± 2.69 m s^{-1}) and returned to the cave at 7.89 ± 4.08 m s^{-1} (airspeed: 7.76 ± 3.82 m s^{-1}) flying with tailwinds, airspeeds that are between their minimum power

speed (6.81 ± 0.21 m s^{-1}) and maximum range speed (11.0 ± 0.35 m s^{-1}). Wind speeds were generally low during the tracking period, with prevailing offshore winds blowing eastward. Bats foraged at ground speeds of 3.95 ± 3.43 m s^{-1} (airspeed: 4.15 ± 3.38 m s^{-1}).

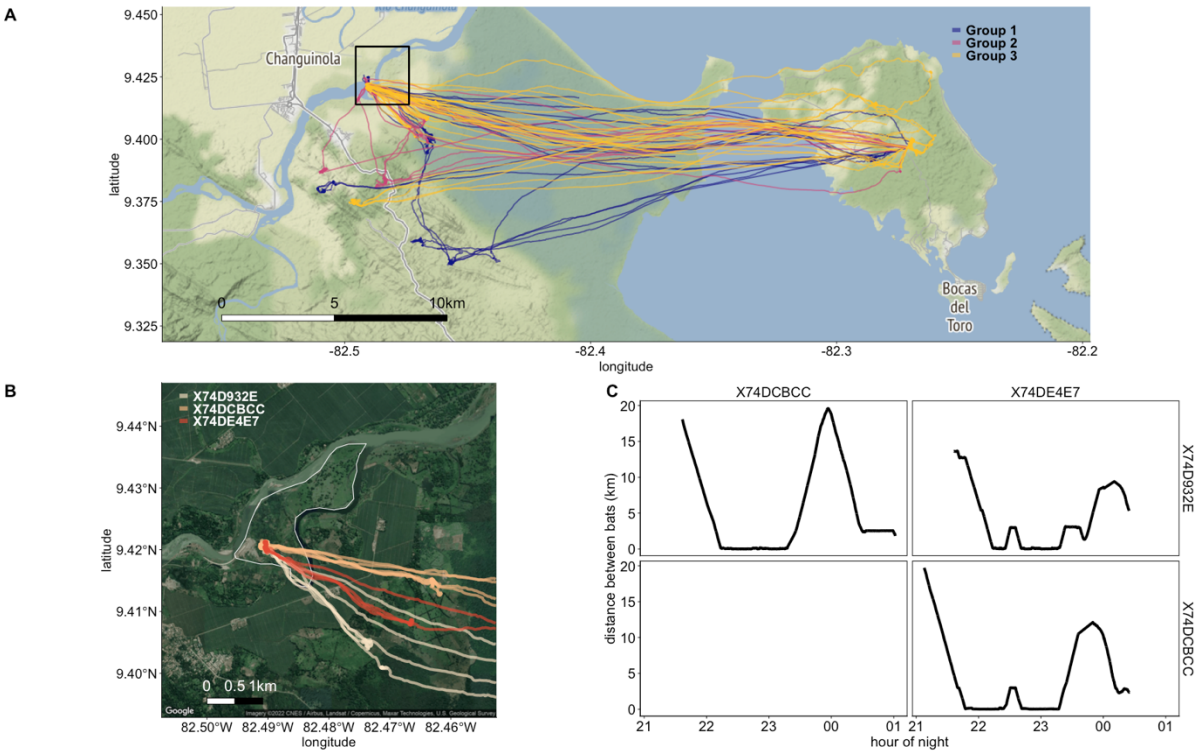

Figure 1. A) Tracking overview with individuals colored by group membership. B) The island in the Changuinola river (Isla Changuinola) shown with three individuals from group 3 on 2016-03-04, and C) the pairwise distances between these three individuals across that night. Note that in C both axes are repeated to show the simultaneous distance between pairs of individuals and the large distances among individuals at the beginning and end of the nights when commuting.

Behavior & foraging patch use

All individuals completed the 25 km commute from the roost to the foraging areas alone (Fig 1C), and individuals were 9.1 ± 5.8 km (mean ± sd) away from one another when commuting. Individuals then converged in the same foraging areas, mostly on the mainland. We only analyzed behaviors other than commuting to look at social influences on them.

Individuals used a mix of moving and resting during the approximately 200 minutes they were outside of the cave, and this did not differ across the three groups (Fig 2A). Bats spent 24.0 ± 19.3% of their time in rest, 24.6 ± 14.6% of time in slow foraging/feeding flights, 31.3 ± 23.6% in faster foraging movements between feeding sites, and 25.1 ± 16.8% of time commuting. We ground-truthed the mainland foraging patches 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 if bats fed on the nectar of *Luehea* flowers, or on the animals attracted to this resource.

Bats used 7.2 ± 4.2 foraging patches (i.e. trees or groups of trees) per night, and patches were 4.0 ± 3.8 km apart. These patches were 23.35 ± 1.4 km from the roost, and only a few foraging patches were used near the roost during the return flight to the cave. As bats increased their total nightly flight distance, they used more patches (Estimate: 0.886 ± 0.034 per additional km, $F_{1, 20.174} = 6.861$, $p = 0.016$, $R^2_m = 0.13$, $R^2_c = 0.70$; Fig S2). Over the course of the night, bats used 20.72 ± 19.91 feeding locations (flower clusters) (range: 3 - 82). However, there was no relationship between the number of feeding clusters they visited within the patches and the number of patches used, or with the time they spent outside the roost (Fig S2).

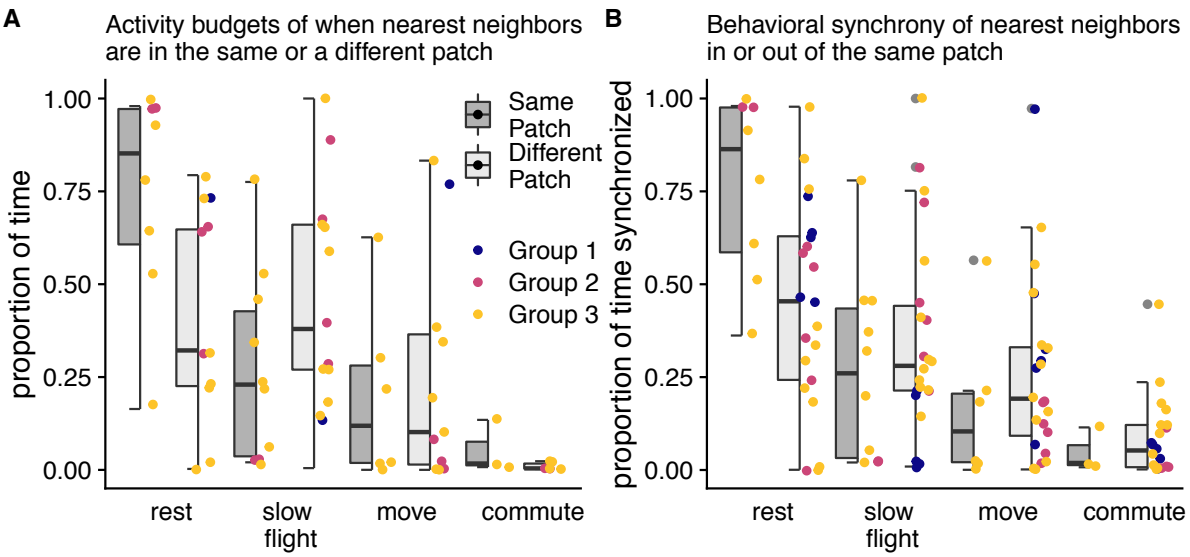

Figure 2. Effects of proximity on bat nightly activity budgets. A) Bat activity budgets when nearest neighbors occupied the same and different patches, but are within 500 m of one another. B) Behavioral synchrony of nearest neighbors in and out of the same patch. Box plots show proportion of time engaged in behaviors for each patch category, and points show the proportions for each individual bat per night.

Activity budgets differed depending on whether individuals were in the same patch as their neighbors or not (Fig 2A-B, Patch Estimate $F_{1,3} = 0.029$; Fig 2). When in the same patch, individuals were 24.3 ± 21.4 m apart (0.25 – 133 m). The proportion of time spent in rest was larger when an individual's nearest neighbor was were in the same patch as their nearest neighbor than when individuals occupied different patches that were within 500 m of one another (same patch (median ± MAD): 85.2 ± 18.6%, different patch: 32.2%± 44.3%, $X^2 = 10.12$, df = 3, p = 0.018, Fig 2A). The proportion within a behavior that was synchronized with a nearest neighbor was not evenly distributed ($X^2 = 4.08$, df = 1, p = 0.043, Fig 2B). Individuals were more likely to be simultaneously engaged in rest when in the same patch as their nearest neighbor that to be synchronized in other behaviors (Fig 2B). Bats rested 19.3 ± 14.3 m away from each other, and resting bouts were longer when they were in closer proximity to another individual, with the strongest effects less than three

meters away (Power Curve / Freundlich Equation intercept = 2.95 ± 0.24 m SE, $p < 0.001$, Fig 3).

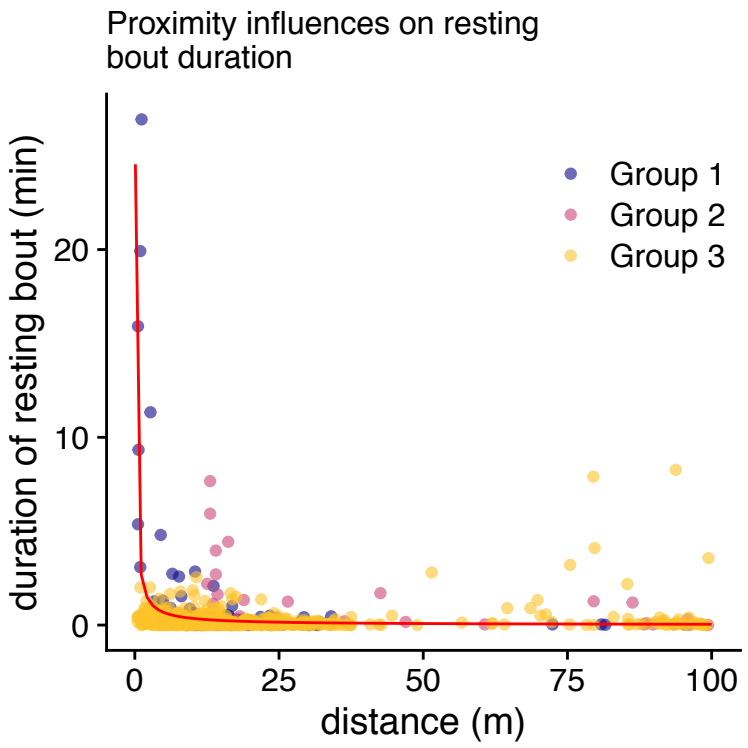

Figure 3. Duration of continuous resting bouts relative to the distance to a bat's nearest neighbor.

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 five different nights (Fig S3). Three other locations on Isla Colón were used repeatedly by a single bat over two nights. The remaining 39 sites were used by one bat on one night each.

Social effects on foraging and resting

Proximity networks of simultaneous GPS locations showed that entire social groups were never in close contact while tracked. There were strongly differentiated spatial relationships among some group members, and the strength centrality and degree of individuals within a

social group was variable among groups (Fig S4). The males tracked as part of this study were never in close proximity to the females from their group, despite similar long-distance commutes. While close proximity between individuals at rest increased the likelihood they would continue resting, there were no overall effects of an individual's strength centrality on overall nightly activity budgets (Fig S5). However, individual strength centrality was positively related to the amount of time that bats were tracked outside of their roost per night (Estimate: 274.58 ± 103.38, $F_{1, 15.62} = 7.054$, $p = 0.018$, $R^2_m = 0.220$, $R^2_c = 0.393$, Fig 3A). There were no effects of strength centrality on foraging efficiency when evaluated using a second order mixed effects model ($F_{2,16.38} = 0.678$, $p = 0.521$, Fig 3B), or on estimated daily energy expenditure ($F_{1,18.18} = 1.52$, $p = 0.245$, Fig 3C).

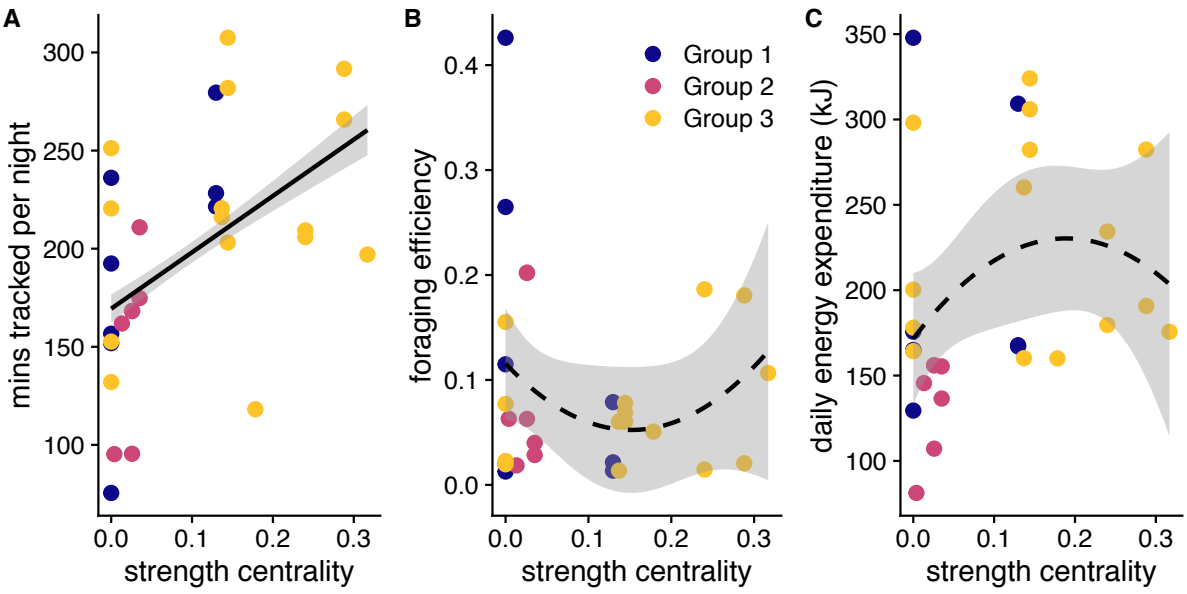

Figure 3. Effects of individual strength centrality on nightly measures of A) duration tracked, B) foraging efficiency, and C) estimated daily energy expenditure. Solid lines indicate statistically significant relationships using a mixed effects model, and dashed lines show relationships that were not significant. Shaded regions show the 95% confidence interval.

Because we tracked social groups sequentially, we were unable to assess if multiple groups are found in the same sites at the same time. However, there was extensive spatial overlap of individuals across the nights of tracking. Proximity networks of GPS locations

that were within 30 m of each other, regardless of time, show overlapping use of foraging and resting locations. We detected three communities from the proximity network created across all tracking nights. These communities link together bats that foraged in the same patches, but at different times and highlights that the same foraging locations host many social groups. Individuals who shared close space at the same time did not necessarily use the same number and constellation of foraging patches. Some individuals did not share space with any other tracked bats, either from their social group or from the other tracked groups (Fig S4).

Energy costs & feeding requirements

The mean minimum power speed of these bats was 6.81 ± 0.21 m s^{-1} and maximum range speed was 11.03 ± 0.34 m s^{-1}. The power curve for each individual bat was used to estimate total metabolic power required for the night. Bat estimated daily energy expenditure (DEE) was 198.47 ± 69.44 kJ per day and increased with tracking time (Estimate: 0.729 ± 0.174, $F_{1,25.61} = 17.462$, $p < 0.001$, $R^2_m = 0.383$, $R^2_c = 0.448$, Fig 4A). This is similar to DEE estimates based on body mass alone of 153.02 ± 5.96 kJ per day (range: 143.07 – 164.89 (Speakman, 2005)) and to doubly-labeled water measurements in *P. hastatus* that were 36% smaller than those at our study site (76.8 ± 6.6 g vs 121.5 ± 7.6 g in this study, estimates from (Kunz et al., 1998) are shown in blue in Fig 4A). We converted the estimated energetic needs for each individual on each tracking night into the number of full *O. pyramidale* flowers required to support that estimated energy expenditure. We found that individuals fed from an increasing number of flower clusters as their total estimated energy needs increased (second order polynomial estimate = 55.45 ± 14.89, 27.73 ±14.86, $F_{2,26.45} = 8.84$, $p = 0.001$, $R^2_m = 0.376$, $R^2_c = 0.494$, Fig 4B). 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.

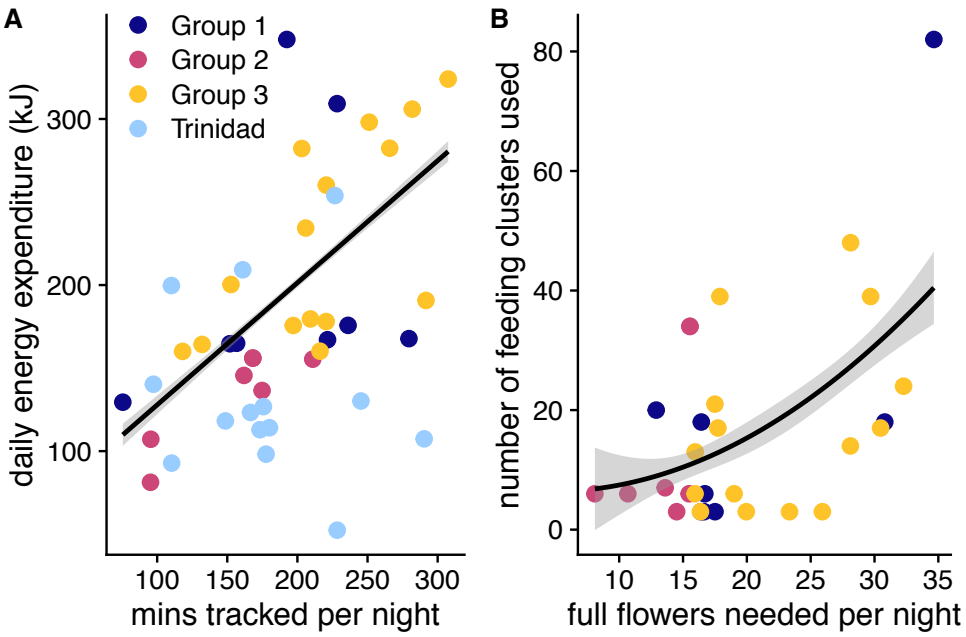

Figure 4. Estimated daily energy expenditure and the estimated energetic returns from foraging. A) Daily energy expenditure and the minutes tracked per night, with comparative data from smaller *P. hastatus* in Trinidad as comparison (Kunz et al., 1998). The line shows the relationship derived from the individuals tracked in this study. B) The number of flowers needed based on average energy content to support the energy requirements of an individual's estimated energy expenditure predict the number of feeding clusters used per night.

Discussion

Based on previous work (Wilkinson and Boughman, 1998), we predicted that *Phyllostomus hastatus* would forage with their social group to feed on *O. pyramidale* flowers. While tracked individuals did use the same foraging areas, most individuals flew to these foraging patches alone instead of commuting with social group members. When individuals were near group members, they tended to rest, and individuals that rested close to one another tended to rest for longer. The strength of their proximity-based networks was not related to measures of foraging success or energy conservation, and it appears that while the main benefit of social foraging is often assumed to be increased foraging success, the bats in

our study rely on social partners during rest. It appears, unlike in the foraging associations of other bat species, resting in *P. hastatus* reinforces social associations or has benefits outside of foraging efficiency such as predator detection.

Social foraging should increase foraging efficiency, either through effects of food detection or social facilitation that increase feeding 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; Dechmann et al., 2010). With increasing group size, Trinidad guppies 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 come at a cost of perceived feeding competition that drives increased bite rates. While we did not directly measure intake rate, we did not find any association between proximity network strength and any foraging metrics. The *P. hastatus* in our study did not modify their foraging, either in the time spent foraging, or the number of foraging patches or feeding locations used in relation to group members.

We found that individual *P. hastatus* from multiple social groups used the same patches of *O. pyramidale*, but arrived at these patches over 25 km from their roost alone. We found that some individuals would reunite with social group members in these patches, while other tended to forage completely on their own and show no spatial or temporal overlap with social group members. This is similar to vampire bats (*Desmodus rotundus*) that fly individually to cattle approximately 300 m away and feed with partners with close social relationships (Ripperger and Carter, 2021). Previous radio tracking work in Trinidad found that during most of the year, social group members did not depart or arrive at the cave together, and tended to forage alone, but on rare occasions joined a group mate in a

nearby foraging area (McCracken and Bradbury, 1981). Members of social groups occupied adjacent foraging ranges and social groups were segregated across the landscape (McCracken and Bradbury, 1981), unlike the large overlap we found in our data. In Trinidad groups were more likely to depart together, and females from the same social group were captured around a *O. pyramidale* feeding site more often than randomly expected during the dry season (Wilkinson and Boughman, 1998). There also appears to be strong social attraction among *P. hastatus* social groups. Social calls broadcast at flowering *O. pyramidale* attracted bats, and social calls from flying *P. hastatus* were most often noted 3-4 hours after sunset when bats were already out foraging (Wilkinson and Boughman, 1998). The higher spatial and temporal resolution of our GPS tracks now indicates they are at least not only attracted to the possibility of food resources, but that they may form resting associations while outside of their roost.

It is possible that at this time of year or within this population in Panama there is more pressure to maintain social associations than to group forage. Within social groups that are structured by kin relationship, strong social bonds between related individuals have numerous life history advantages (Silk, 2007), extending lifespans (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). However, on Trinidad, female *P. hastatus* form stable, relatively closed groups of unrelated females that stay together for their lifetime and show highly developed social bonds (McCracken and Bradbury, 1981; Wilkinson et al., 2016). They develop group-specific social calls (Boughman, 1997; Wilkinson and Boughman, 1998), and recognize and guard group-members' offspring (Bohn et al., 2009; Bohn et al., 2007). Low reproductive rates and high infant mortality in this species (Stern and Kunz, 1998) are strong selective pressures on potential cooperation among unrelated females. The conditions structuring *P. hastatus* social groups may be similar to groups of unrelated females in wild equids (Cameron et al.,

2009) and cooperative breeding birds (Riehl and Strong, 2018). Close rest while foraging, rather than feeding together, may be one way for the bats to reinforce their social bonds since *P. hastatus* has not been observed to engage in the extended grooming that characterizes social bond maintenance in other mammals (Kern and Radford, 2021; Silk et al., 2003; Wilkinson, 1986), or to potentially guard against predation.

Alternatively, there could be regional differences in the main drivers on social group formations depending on the resource landscape. On Trinidad it has been hypothesized that recruitment of group members to flowering trees may predominantly help bats defend trees against competitors (Wilkinson and Boughman, 1998). However, in Panamá 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 per night provides approximately 600 kJ of energy at the beginning of the night 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 per day, indicating that a single *O. pyramidale* crown could support the daily energy needs of 3 - 7 bats. Such a limited resource may be worth defending from conspecifics if all available flowers could be fully exploited (Wilkinson and Boughman, 1998), but would not support the needs of an entire social group of bats without moving to several patches to feed. The closest spatial associations among foraging group members did not occur in the feeding patches, suggesting that a collective resource defense is not the likely explanation for foraging and resting near group mates for this population in Panamá.

Instead, 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 traveled and potential weather hazards. Nectar and fruit-feeding fruit bats appear to have large and robust cognitive maps of their (Harten et al., 2020; Toledo et al., 2020). These species will 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 non-overlapping ranges may be developed through reinforcement learning that minimizes competition (Goldshtein et al., 2020).

On the other hand, social groups of *P. hastatus* seem to seek out one another while foraging away from their cave roosting site. Individuals commuted separately to a foraging area, and tended to only synchronize their behavior when resting. These individuals were exploiting the same resources, but did not seem to do so in a coordinated way. *Phyllostomus hastatus* were previously found to forage within 10 km of their (McCracken and Bradbury, 1981; William and Williams, 1970), and most will successfully navigate back to their home roost after displacement of up to 20-25 km. At 30 km, however, bats searched seemingly randomly, then returned to the release point, repeating this process up to four times, and rarely returned when displaced 50 km or more (William and 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. This is particularly true since they had to cross the sea and large commercial banana farms to reach these areas. All of our tracked bats foraged in areas with *O. pyramidale*, where on their home island and other nearby mainland locations *O. pyramidale* was not yet available. This far-removed distance suggests that once an *O. pyramidale* patch is discovered, the social information quickly moves through a colony bringing social group members together in foraging areas. *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 and Boughman, 1998). It is unknown if this is due to shortage of other food sources or to a preference for nectar, but locating this widely distributed food

source may rely on social information transfer. This may be a rare, but crucial resource during the transition period when few trees are flowering or in fruit, and finding food is more unpredictable. Further tracking and detailed dietary analysis are needed to identify how and when bats switch between food resources and the behavioral and energetic correlates of this change.

Data availability

The full GPS data set and code is available from the Movebank Data Repository (doi released on acceptance, code and data with environmental and behavioral annotation is available at Dryad for review (https://datadryad.org/stash/share/DBJdu_DVmEVBp6Yeq5x2RwupCy6W9NOaprjDtUZIH3E).

References

Barocas A, Ilany A, Koren L, Kam M, Geffen E, 2011. Variance in centrality within rock hyrax social networks predicts adult longevity. PLoS One 6:e22375. doi: 10.1371/journal.pone.0022375.

Author. 2016. MuMIn: Multi-Model Inference.

Bates D, Mächler M, Bolker B, Walker S, 2015. Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1-48. doi: 10.18637/jss.v067.i01.

Beauchamp G, Heeb P, 2001. Social foraging and the evolution of white plumage. Evol Ecol Res 3:703-720.

Bell WJ, 1990. Searching Behaviour: The behavioural ecology of finding resources. London: Chapman and Hall.

Berdahl A, Torney C, Ioannou C, Faria J, Couzin I, 2013. Emergent sensing of complex environments by mobile animal groups. Science 339:574-576. doi: 10.1126/science.1225883.

Bhattacharya K, Vicsek T, 2014. Collective foraging in heterogeneous landscapes. J R Soc Interface 11:20140674. doi: 10.1098/rsif.2014.0674.

Bohn KM, Moss CF, Wilkinson GS, 2009. Pup guarding by greater spear-nosed bats. Behav Ecol Sociobiol 63:1693-1703. doi: 10.1007/s00265-009-0776-8.

Bohn KM, Wilkinson GS, Moss CF, 2007. Discrimination of infant isolation calls by female greater spear-nosed bats, *Phyllostomus hastatus*. Anim Behav 73:423-432. doi: 10.1016/j.anbehav.2006.09.003.

Boughman J, Wilkinson G, 1998. Greater spear-nosed bats discriminate group mates by vocalizations. Anim Behav 55:1717-1732. doi: 10.1006/anbe.1997.0721.

Boughman JW, 1997. Greater spear-nosed bats give group-distinctive calls. Behav Ecol Sociobiol 40:61-70. doi: 10.1007/s002650050316.

Boughman JW, 1998. Vocal learning by greater spear-nosed bats. Proc R Soc B 265:227-233. doi: 10.1098/rspb.1998.0286.

Boughman JW, 2006. Selection on social traits in greater spear-nosed bats, Phyllostomus hastatus. Behav Ecol Sociobiol 60:766-777. doi: 10.1007/s00265-006-0220-2.
Calderón-Capote MC, Dechmann DKN, Fahr J, Wikelski M, Kays R, O'Mara MT, 2020. Foraging movements are density-independent among straw-coloured fruit bats. R Soc Open Sci 7. doi: 10.1098/rsos.200274.
Cameron EZ, Setsaas TH, Linklater WL, 2009. Social bonds between unrelated females increase reproductive success in feral horses. Proc Natl Acad Sci U S A 106:13850-13853. doi: 10.1073/pnas.0900639106.
Clauset A, Newman ME, Moore C, 2004. Finding community structure in very large networks. Phys Rev E Stat Nonlin Soft Matter Phys 70:066111. doi: 10.1103/PhysRevE.70.066111.
Conradt L, Roper TJ, 2005. Consensus decision making in animals. Trends Ecol Evol 20:449-456.
Dechmann D, Heucke S, Giuggioli L, Safi K, Voigt C, Wikelski M, 2009. Experimental evidence for group hunting via eavesdropping in echolocating bats. Proc R Soc B 276:2721-2728. doi: 10.1098/rspb.2009.0473.
Dechmann D, Kranstauber B, Gibbs D, Wikelski M, 2010. Group hunting-a reason for sociality in molossid bats? PLoS One 5:e9012. doi: 10.1371/journal.pone.0009012.
Egert-Berg K, Hurme ER, Greif S, Goldstein A, Harten L, Herrera ML, Flores-Martinez JJ, Valdes AT, Johnston DS, Eitan O, Borissov I, Shipley JR, Medellin RA, Wilkinson GS, Goerlitz HR, Yovel Y, 2018. Resource ephemerality drives social foraging in bats. Curr Biol 28:3667-3673. doi: 10.1016/j.cub.2018.09.064.
Farine DR, 2013. Animal social network inference and permutations for ecologists in R using asnipe. Methods Ecol Evol 4:1187-1194.
Fenton MB, 2003. Eavesdropping on the echolocation and social calls of bats. Mammal Rev 33:193-204. doi: 10.1046/j.1365-2907.2003.00019.x.
Frere CH, Krutzen M, Mann J, Connor RC, Bejder L, Sherwin WB, 2010. Social and genetic interactions drive fitness variation in a free-living dolphin population. Proc Natl Acad Sci USA 107:19949-19954. doi: 10.1073/pnas.1007997107.
Giraldeau L, Beauchamp G, 1999. Food exploitation: searching for the optimal joining policy. Trends Ecol Evol 14:102-106.
Goldshtein A, Handel M, Eitan O, Bonstein A, Shaler T, Collet S, Greif S, Medellín RA, Emek Y, Korman A, Yovel Y, 2020. Reinforcement learning enables resource partitioning in foraging bats. Curr Biol. doi: 10.1016/j.cub.2020.07.079.
Hahsler M, Piekenbrock M, Doran D, 2019. dbscan: Fast Density-Based Clustering with R. J Stat Softw 91. doi: 10.18637/jss.v091.i01.
Harten L, Katz A, Goldshtein A, Handel M, Yovel Y, 2020. The ontogeny of a mammalian cognitive map in the real world. Science 369:194-197. doi: 10.1126/science.aay3354.
Hedenström A, 2003. Twenty-Three Testable Predictions About Bird Flight. In: Berthold P, Gwinner E, Sonnenschein E, editors. Avian Migration Berlin: Springer. p. 563-582.
Author. 2020. fpc: Flexible Procedures for Clustering. Version R package version 2.2-5.
Kays R, Rodríguez M, Valencia L, Horan… R, 2012. Animal visitation and pollination of flowering balsa trees (*Ochroma pyramidale*) in Panama. Mesoamericana 16:54-70.
Kern JM, Radford AN, 2021. Strongly bonded individuals prefer to forage together in cooperatively breeding dwarf mongoose groups. Behav Ecol Sociobiol 75. doi: 10.1007/s00265-021-03025-0.
Kranstauber B, Kays R, Lapoint S, Wikelski M, Safi K, 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. J Anim Ecol 81:738-746. doi: 10.1111/j.1365-2656.2012.01955.x.
Kunz TH, Robson SK, Nagy KA, 1998. Economy of harem maintenance in the greater spear-nosed bat, *Phyllostomus hastatus*. J Mammal:631-642.
Kuznetsova A, Brockhoff PB, Christensen RHB, 2017. lmerTest Package: Tests in Linear Mixed Effects Models. J Stat Softw 82. doi: 10.18637/jss.v082.i13.

McClintock BT, Michelot T, Goslee S, 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. Methods Ecol Evol 9:1518-1530. doi: 10.1111/2041-210x.12995.
McCracken GF, Bradbury JW, 1981. Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. Behav Ecol Sociobiol 8:11-34. doi: 10.1007/Bf00302840.
McInnes AM, McGeorge C, Ginsberg S, Pichegru L, Pistorius PA, 2017. Group foraging increases foraging efficiency in a piscivorous diver, the African penguin. R Soc Open Sci 4:170918. doi: 10.1098/rsos.170918.
McNab BK, 1969. The economics of temperature regulation in neotropical bats. Comp Biochem Physiol 31:227-268. doi: 10.1016/0010-406X(69)91651-X.
Michelot T, Langrock R, Bestley S, Jonsen ID, Photopoulou T, Patterson TA, 2017. Estimation and simulation of foraging trips in land-based marine predators. Ecol 98:1932-1944. doi: 10.1002/ecy.1880.
O'Mara M, Dechmann D, Page R, 2014a. Frugivorous bats evaluate the quality of social information when choosing novel foods. Behavioral Ecology 25:1233-1239. doi: 10.1093/beheco/aru120.
O'Mara MT, Amorim F, Scacco M, McCracken GF, Safi K, Mata V, Tome R, Swartz S, Wikelski M, Beja P, Rebelo H, Dechmann DKN, 2021. Bats use topography and nocturnal updrafts to fly high and fast. Curr Biol 31:1311-1316 e1314. doi: 10.1016/j.cub.2020.12.042.
O'Mara MT, Scharf AK, Fahr J, Abedi-Lartey M, Wikelski M, Dechmann DKN, Safi K, 2019. Overall dynamic body acceleration in straw-colored fruit bats increases in headwinds but not with airspeed. Front Ecol Evol 7:200. doi: 10.3389/fevo.2019.00200.
O'Mara MT, Wikelski M, Dechmann DKN, 2014b. 50 years of bat tracking: device attachment and future directions. Methods Ecol Evol 5:311-319. doi: 10.1111/2041-210x.12172.
O'Mara MT, Wikelski M, Voigt CC, Ter Maat A, Pollock HS, Burness G, Desantis LM, Dechmann DK, 2017. Cyclic bouts of extreme bradycardia counteract the high metabolism of frugivorous bats. eLife 6:e26686. doi: 10.7554/eLife.26686.
Page R, Ryan M, 2006. Social transmission of novel foraging behavior in bats: frog calls and their referents. Curr Biol 16:1201-1205. doi: 10.1016/j.cub.2006.04.038.
Pennycuick CJ, 2008. Modelling the flying bird. London: Academic Press.
Author. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna Austria.
Ramakers JJC, Dechmann DKN, Page RA, O'Mara MT, 2016. Frugivorous bats prefer information from novel social partners. Anim Behav 116:83-87. doi: 10.1016/j.anbehav.2016.03.021.
Ranacher P, Brunauer R, Trutschnig W, Van der Spek S, Reich S, 2016. Why GPS makes distances bigger than they are. Int J Geogr Inf Sci 30:316-333. doi: 10.1080/13658816.2015.1086924.
Ratcliffe J, ter Hofstede H, 2005. Roosts as information centres: social learning of food preferences in bats. Biol Lett 1:72-74. doi: 10.1098/rsbl.2004.0252.
Riehl C, Strong MJ, 2018. Stable social relationships between unrelated females increase individual fitness in a cooperative bird. Proc R Soc B 285. doi: 10.1098/rspb.2018.0130.
Ripperger SP, Carter GG, 2021. Social foraging in vampire bats is predicted by long-term cooperative relationships. PLoS Biol 19:e3001366. doi: 10.1371/journal.pbio.3001366.
Robitaille AL, Webber QMR, Vander Wal E, Golding N, 2019. Conducting social network analysis with animal telemetry data: Applications and methods using spatsoc. Methods Ecol Evol 10:1203-1211. doi: 10.1111/2041-210x.13215.
Safi K, Kranstauber B, Weinzierl R, Griffin L, Rees EC, Cabot D, Cruz S, Proano C, Takekawa JY, Newman SH, Waldenstrom J, Bengtsson D, Kays R, Wikelski M,

Bohrer G, 2013. Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. Mov Ecol 1:4. doi: 10.1186/2051-3933-1-4.

Samuni L, Crockford C, Wittig RM, 2021. Group-level cooperation in chimpanzees is shaped by strong social ties. Nat Commun 12:539. doi: 10.1038/s41467-020-20709-9.

Schubert E, Sander J, Ester M, Kriegel HP, Xu X, 2017. DBSCAN Revisited, Revisited. ACM Transactions on Database Systems 42:1-21. doi: 10.1145/3068335.

Schülke O, Bhagavatula J, Vigilant L, Ostner J, 2010. Social bonds enhance reproductive success in male macaques. Curr Biol 20:2207-2210. doi: 10.1016/j.cub.2010.10.058.

Silk JB, 2007. The adaptive value of sociality in mammalian groups. Philos Trans R Soc B 362:539-559. doi: 10.1098/rstb.2006.1994.

Silk JB, Alberts SC, Altmann J, 2003. Social bonds of female baboons enhance infant survival. Science 302:1231-1234.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL, 2010. Strong and consistent social bonds enhance the longevity of female baboons. Curr Biol 20:1359-1361. doi: 10.1016/j.cub.2010.05.067.

Snijders L, Krause S, Tump AN, Breuker M, Ortiz C, Rizzi S, Ramnarine IW, Krause J, Kurvers R, 2021. Causal evidence for the adaptive benefits of social foraging in the wild. Commun Biol 4:94. doi: 10.1038/s42003-020-01597-7.

Speakman J, 2005. Body size, energy metabolism and lifespan. Journal of Experimental Biology 208:1717-1730. doi: 10.1242/jeb.01556.

Stern AA, Kunz TH, 1998. Intraspecific variation in postnatal growth in the greater spear-nosed bat. J Mammal 79:755. doi: 10.2307/1383086.

Stilz WP, Schnitzler HU, 2012. Estimation of the acoustic range of bat echolocation for extended targets. J Acoust Soc Am 132:1765-1775. doi: 10.1121/1.4733537.

Thomas SP, 1975. Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. J Exp Biol 63:273-293.

Toledo S, Shohami D, Schiffner I, Lourie E, Orchan Y, Bartan Y, Nathan R, 2020. Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system. Science 369:188-193. doi: 10.1126/science.aax6904.

Valone TJ, 1989. Group foraging, public information, and patch estimation. Oikos:357-363.

von Busse R, Swartz SM, Voigt CC, 2013. Flight metabolism in relation to speed in Chiroptera: testing the U-shape paradigm in the short-tailed fruit bat *Carollia perspicillata*. J Exp Biol 216:2073-2080. doi: 10.1242/jeb.081760.

Ward S, Moller U, Rayner JM, Jackson DM, Bilo D, Nachtigall W, Speakman JR, 2001. Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris*. J Exp Biol 204:3311-3322.

Wilkinson G, Boughman J, 1998. Social calls coordinate foraging in greater spear-nosed bats. Anim Behav 55:337-350.

Wilkinson GS, 1986. Social grooming in the common vampire bat, *Desmodus rotundus*. Anim Behav 34:1880-1889.

Wilkinson GS, Carter GG, Bohn KM, Adams DM, 2016. Non-kin cooperation in bats. Philos Trans R Soc B 371. doi: 10.1098/rstb.2015.0095.

William TC, Williams JM, 1970. Radio tracking of homing and feeding flights of a neotropical bat, *Phyllostomus hastatus*. Anim Behav 18:302-309. doi: 10.1016/s0003-3472(70)80042-2.

Wright GS, 2016. Social Learning and Information Transfer in Bats: Conspecific Influence Regarding Roosts, Calls, and Food. In: Ortega J, editor. Sociality in Bats: Springer. p. 211-230.

Wyman MT, Pinter-Wollman N, Mooring MS, Hayes L, 2021. Trade-offs between fighting and breeding: a social network analysis of bison male interactions. J Mammal. doi: 10.1093/jmammal/gyaa172.

Supplemental Information

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Table S1. Biometric and tracking information for the individuals analyzed in this study. Reproductive state is coded as nr: non-reproductive, plac: post-lactation, and nulli: nulliparous. Nightly values for the minutes of tracking and number of locations used are given for means ± sd when more than one night was recorded.

Bat ID	Network Label ID	Group ID	Sex	Reproductive State	Mass (g)	Forearm length (mm)	Wing length (mm)	Wing area (mm2)	Nights Analyzed	Time Analyzed (min)	Number of Locations Used	Strength Centrality	Degree
2016030703	1	one	m	nr	134	93.5	271.96	22966.52	2	133.99 ± 82.68	7296.5 ± 3939.29	0	0
2016030705	2	one	f	plac	124	87.8	280.82	24543.47	1	156.67	7694	0	0
71A0D95	3	one	f	nulli	122	89.9	282.74	24088.56	2	224.89 ± 4.82	12371.5 ± 1289.06	0.13	1
71A111A	4	one	f	nulli	109	90.8	296.86	25587.39	1	279.52	16752	0.13	1
74DDA80	5	one	f	nulli	123	91.2	278.44	23724.58	1	151.88	6268	0	0
74DE9A7	6	one	f	plac	122	91.5	274.95	23752.23	1	236.13	13488	0	0
74D8954	7	two	f	plac	128	93.02	317.17	29422.44	1	161.88	6211	0.178	3
74DA92F	8	two	f	plac	109	87.6	250.07	19667.46	2	192.87 ± 25.53	6767 ± 1236.02	0.24	5
74DCA83	10	two	f	nulli	123	92.1	300.31	29703.42	2	131.85 ± 51.45	5028 ± 2224.56	0.004	1
74D8C25	11	three	f	nulli	131	93.2	308.25	28074.65	1	118.15	5158	0.288	5
74D932E	12	three	f	nulli	116	93.6	304.29	28397.6	2	207.63 ± 2.4	8783 ± 83.44	0.317	5
74DAF9C	9	three	f	nulli	126	94.5	296.29	26317.99	1	95.27	5628	0	0
74DCBCC	13	three	f	plac	114	89.7	289.26	22936.64	2	278.75 ± 18.27	11910 ± 1578.26	0	0
74DE4E7	14	three	f	plac	124	94.2	296.11	26383.96	1	197.03	6618	0.144	4
74F7D4C	15	three	m	nr	137	93.2	277.12	23586.97	1	152.63	3748	0.137	4
74F8E19	16	three	f	plac	113	91.7	289.38	25321.02	3	201.26 ± 61.87	7702.67 ± 2597.55	0.013	2
74F9F83	17	three	f	plac	116	92	284.51	24720.16	3	264.17 ± 54.4	7866.33 ± 1690.4	0.035	2
74FE24E	18	three	f	plac	113	91.7	270.5	22057.56	2	218.35 ± 3.15	7528 ± 622.25	0.026	1

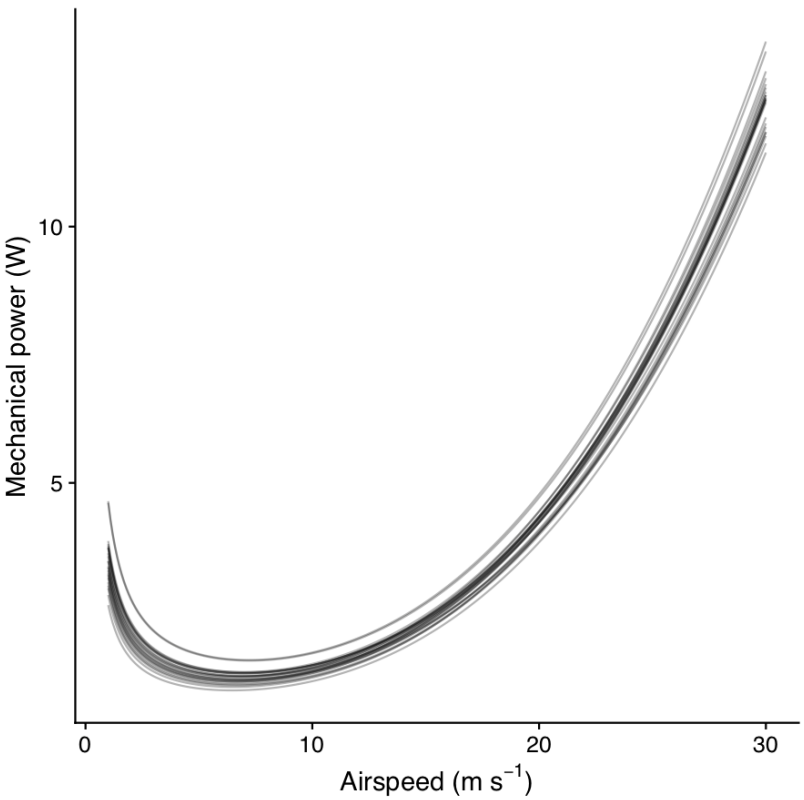

Figure S1. Mechanical power requirements at airspeeds for each bat in this study. Power output was calculated following Pennycuick (2008) at 50 m and 25°C using each individual's body mass and wing dimensions.

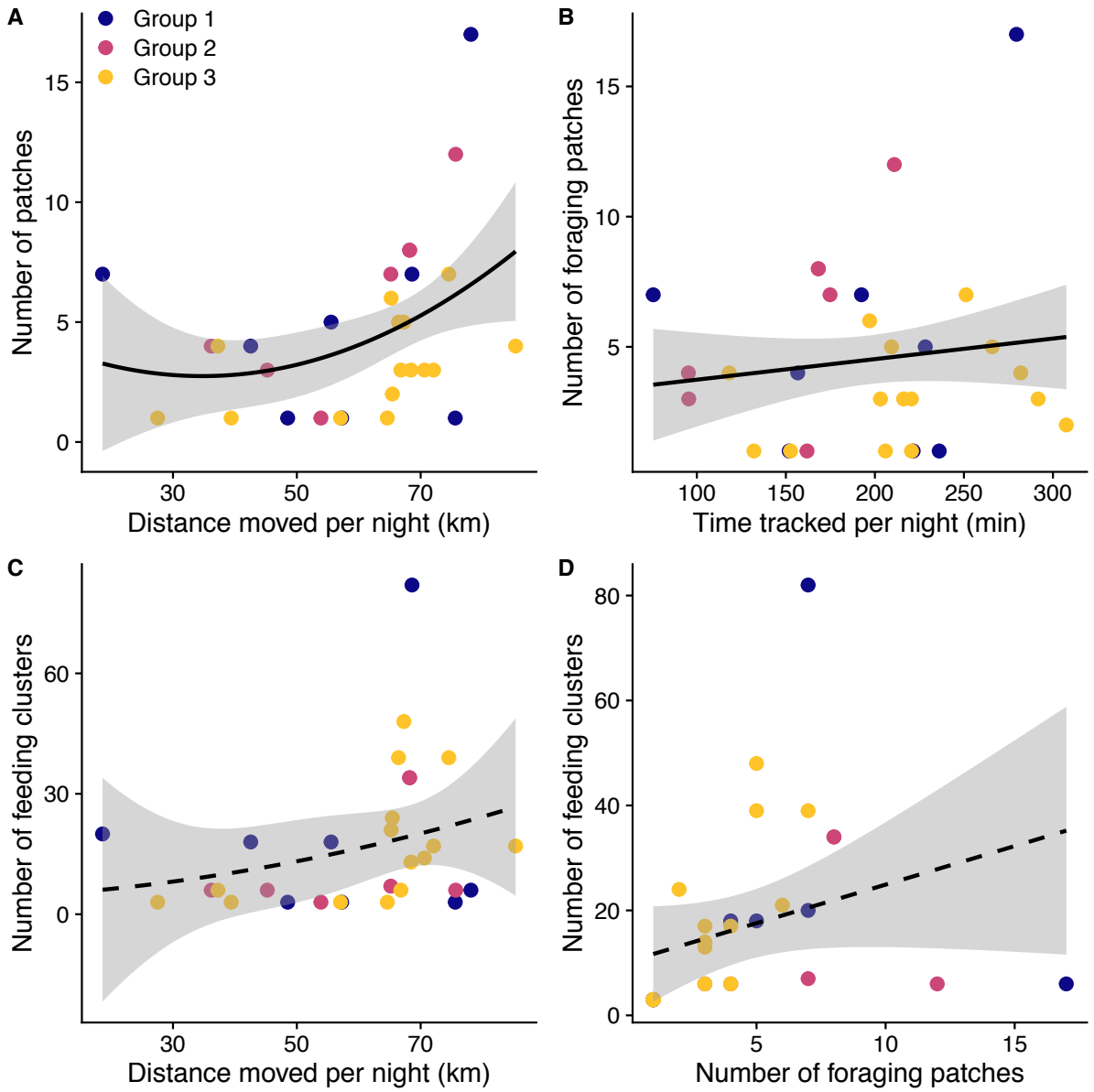

Figure S2. The number of foraging patches used is predicted by A) the distance that individuals moved each night and B) the total time that individuals were tracked each night. The number of feeding clusters identified was not predicted by either C) the distance moved per night or D) the number of foraging patches used. Statistically significant slopes that differed from zero are shown by solid lines, non-significant slopes by dashed lines, and shaded areas indicate 95% confidence intervals.

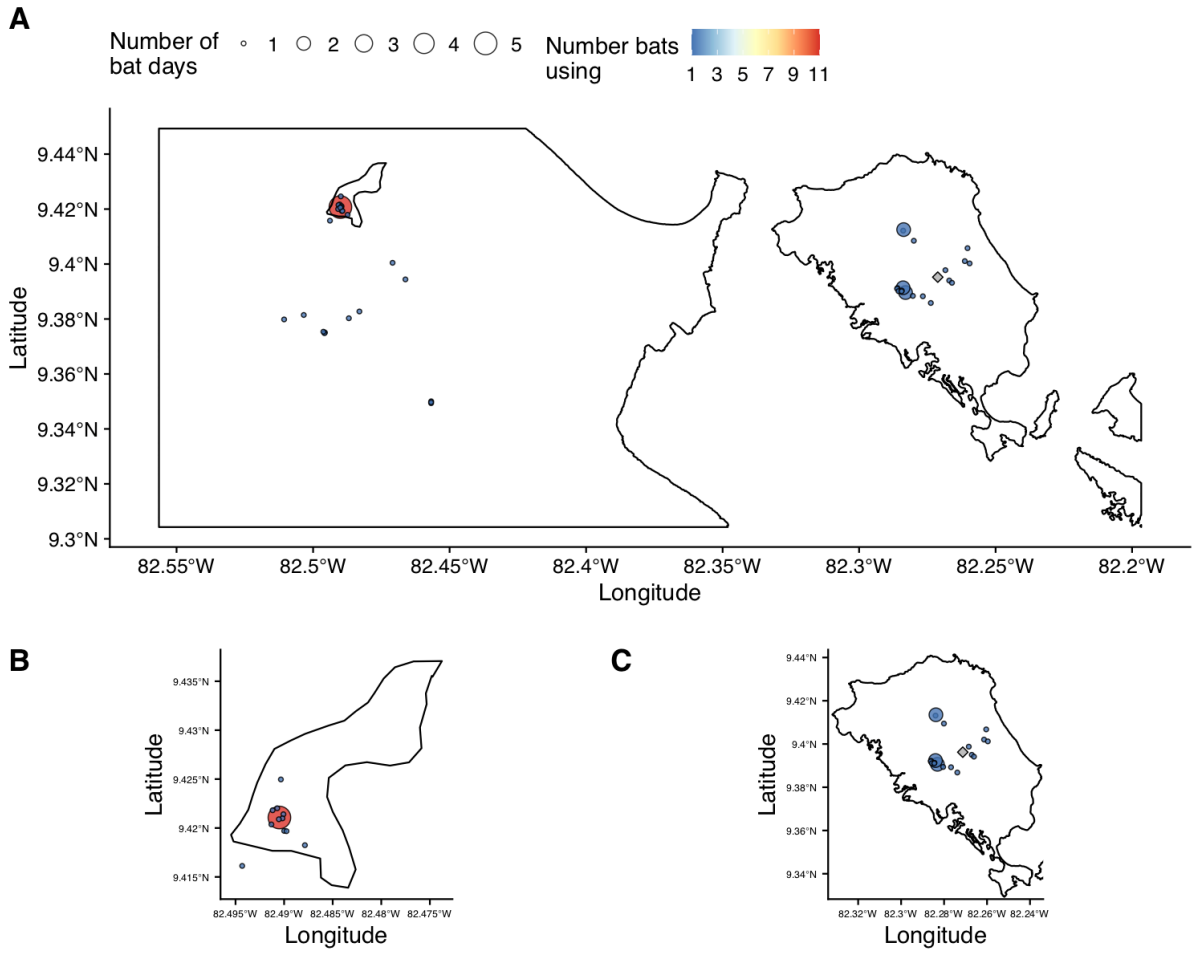

Figure S3. Resting patches clustered from GPS locations. A) Resting patches are shown across the study area, scaled by the number of individual bat days that the sites were used and colored by the number of individual bats that used the patch. Resting patches are shown for B) Isla Changuinola, and C) Isla Colón.

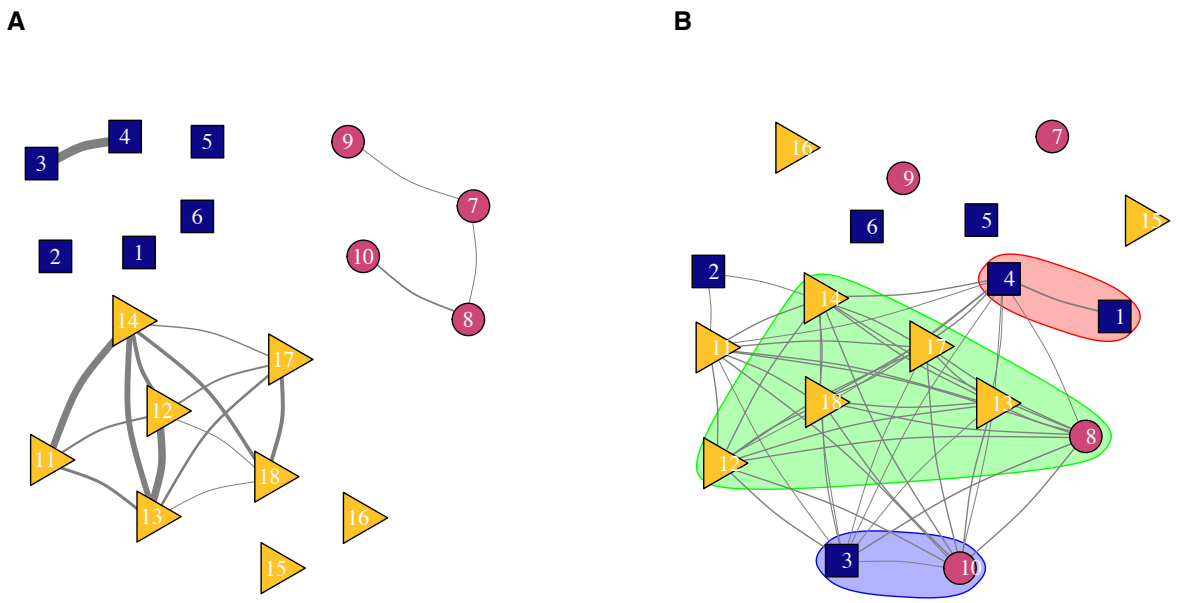

Figure S4. A) Proximity networks of simultaneous spatial associations (same space, same time). Edge weights show strength centrality, and note that individuals 1 and 15 are males. B) networks of across-night foraging patch associations (same space, different time). Individual bats are shown as part of their social group (group 1: blue square, group 2: green circle, group 3: yellow triangle. Foraging patch communities are highlighted by the size of their membership (community 1: red, community 2: green, community 3: purple).

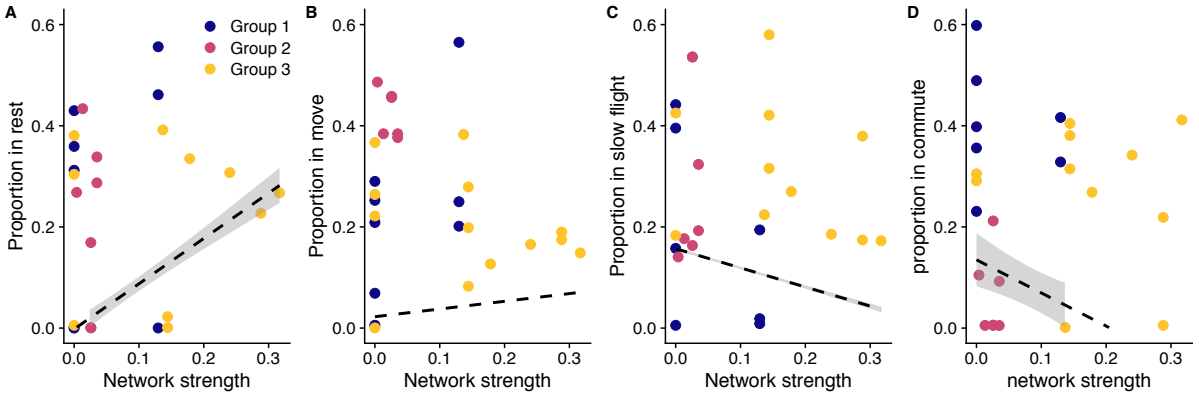

Figure S5. Relationships between proximity network strength of individual bats and the proportion of time that they spend per night while A) Resting, B) Moving between patch, C) slow foraging and feeding flight, and D) Commuting.