Resting together, foraging apart: Network structure of foraging bats is not explained by energy expenditure or foraging efficiency

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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. To test this, we tracked individuals in three social groups of *Phyllostomus hastatus* (greater spear-nosed bats) in Bocas del Toro, Panamá. *Phyllostomus hastatus* seasonally feed on balsa flowers, and group-specific social calls are hypothesized to coordinate social foraging. We found that bats commuted alone but then joined group members in small foraging patches with high densities of flowering balsas, approximately 25 km from their roost. Their estimated energy expenditure was not related to their proximity social network, and network strength did not predict foraging efficiency. Bats in the same foraging patch did not coordinate foraging movement, but close proximity among individuals increased resting bout duration and synchrony. Bats across all social groups used the same resting areas, potentially due to the resting site's physical characteristics, proximity to abundant food resources or predation avoidance. These results indicate that factors other than increased feeding efficiency may structure network relationship of group members while foraging.

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). Even in robot swarms, social cues are more heavily weighed when food density is low, forcing the robots to cooperate (Liu et al., 2007). Social foraging may thus play an important role for the formation and stability of groups in animals foraging on patchy and/or unpredictable resources.

Foraging in groups can convey energetic benefits by increasing foraging success and make energy intake more predictable (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 prey (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 social groups foraging together during a period of low resource abundance but high resource specificity, 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). These omnivorous bats have diverse diets, but during the dry season when fruit availability is low, they feed nearly exclusively on the nectar of balsa trees (*Ochroma pyramidale*). These 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). 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. We hypothesized that if *P. hastatus* social groups forage together to increase food intake, then animals with closer proximity network connections should forage in the same food patches more often, and there should be a positive relationship between network strength, increased foraging efficiency, and decreased nightly energy expenditure. However, we show that social associations are largely independent of foraging, and instead resting bout durations increased when animals were close to one another.

Methods

Adult *Phyllostomus hastatus* (n=40, 38 F / 2 M) from three social groups were captured from their roosts in ceiling depressions in a cave (“La Gruta”) on Isla Colón, Bocas del Toro, Panamá using a bucket trap. Both males were adult harem males, and the females

comprised 15 nulliparous young females, and 19 postlactating females. Bats 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. Wing photos were taken of one fully outstretched wing placed flat over mm graph paper to measure wing dimensions for flight power estimates. A subset of bats from each group were fitted with a GPS data logger (Gypsy-5 GPS, TechnoSmArt, Rome, Italy, (O'Mara et al., 2021)) that was wrapped in a 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 %). Thirty-seven tags were deployed across all groups (Group 1: 14 deployed, 5 F / 1 M recovered; Group 2: 6 deployed, 4 F recovered; Group 3: 17 deployed, 8 F / 1M recovered).

GPS tags were programmed to collect location fixes from 18 h – 06 h local time at a frequency of 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 19 recovered tags collected one to four nights of data for a total of 34 bat nights, with a range of 31.7 – 318.42 min of data collected per night (mean ± sd: 186.46 ± 73.39). We removed from analysis five nights of tracking from five different bats that were short for various reasons (e.g., the bat remained in the cave for most of the night draining the battery), leaving 29 bat nights from 18 females.

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

Ground speed, wind speed, and wind accommodation.

Ground speed and bearing were calculated for successive time points in *move* (Kranstauber et al., 2012). We then annotated the GPS data using a weighted interpolation

of the U and V components of wind to match the resolution of the GPS sampling to calculate the wind support and crosswind for each location (O'Mara et al., 2021; O'Mara et al., 2019; Safi et al., 2013).

Behavioral segmentation

To identify behavioral states of roosting, 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 angles. Models were fit for each bat on each night it was tracked (a bat night). The track for each bat night was regularized to one second intervals using a correlated random walk procedure (*momentuHMM::crawlWrap*) and then passed to the hidden Markov model. Simulations to target the number of identifiable states (McClintock et al., 2018) (Michelot et al., 2017) 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.

A patch (either foraging or resting) was defined as a cluster of concentrated 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) in *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 *dbscan*::*kNNdistplot* (Hahsler and Piekenbrock, 2017). To facilitate comparisons across all individual bat nights, patches with centroids that were less than 30 m apart were lumped together as a single patch.

Once foraging patches were identified, we then further classified clusters of points into 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*.

Energy expenditure

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 ± 0.345 m s^{-1}. 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 foraging returns, 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 networks

We constructed proximity-based social networks in *spatsoc* (Robitaille et al., 2019). GPS fixes were grouped to one-minute intervals, and proximity was assessed at a distance of 30 m. This is twice the spatial error of a stationary tag (14.22 ± 12.05 m (O'Mara et al., 2021)),

although this error decreases dramatically when in flight (Ranacher et al., 2016), and 30 m is slightly larger than the approximate diameter of a balsa crown. We then calculated network strength, centrality, and closeness in *asnipe* (Farine, 2013) using a simple ratio index. All three measures were highly correlated with each other, and to simplify analysis we used the network strength of each individual in subsequent analyses. Network strength is the sum of all edge weights connected to the focal individual, and is a reasonable metric for time and effort spent in close proximity (Wyman et al., 2021). The proximity networks showed large amounts of variation within and among the groups in how much time was spent in close proximity, with individuals of some groups not showing any locations near another tagged individual. To identify if there were spatial locations that were used by bats across the social groups, we used fast-greedy community detection in *igraph* (Clauset et al., 2004). These networks then show how spatial location can connect individuals and groups across time.

All analyses were conducted in R 4.02 (R Core Team, 2020). Generalized linear mixed effects models were fit in *lme4* with individual as a random intercept (Bates et al., 2015), and significance of fixed effects was tested with a likelihood ratio test of nested models. Marginal R^2 for the fixed effects were calculated in *MuMIn* (Bartoń, 2016). 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).

Results

Tracking Summary

The 18 tracked females 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, and 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 a tailwind 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 a tailwind. 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}).

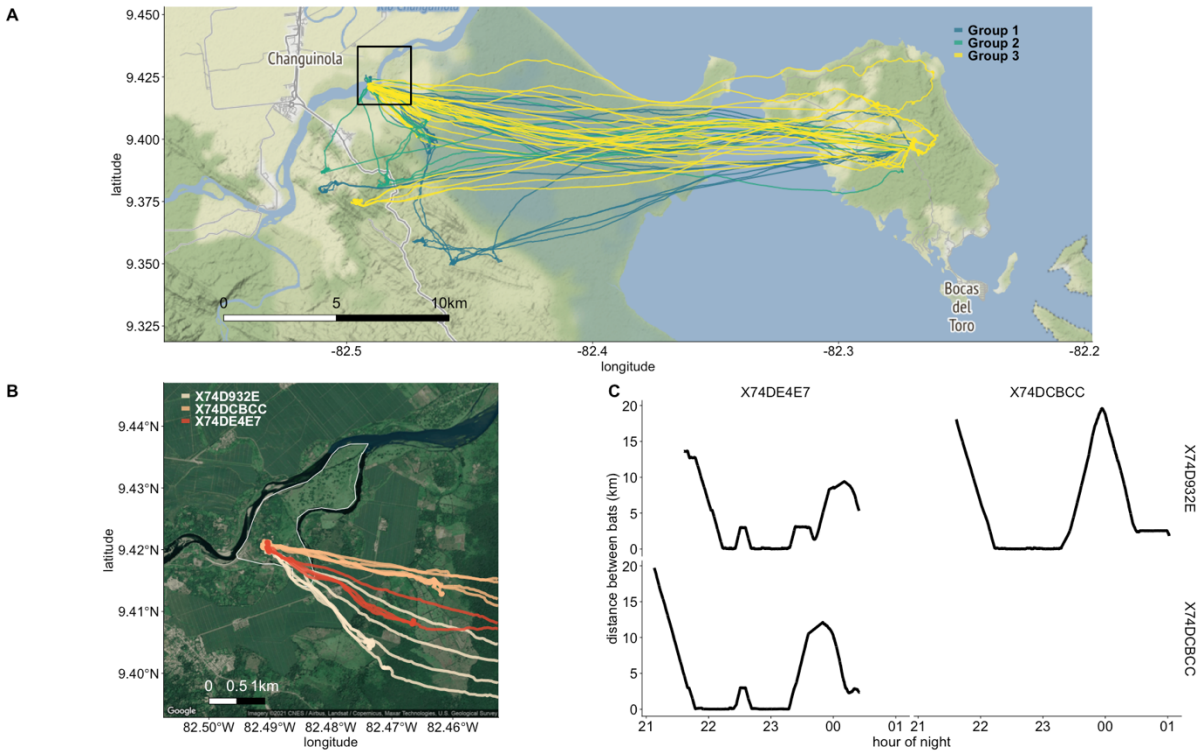

Figure 1. A) Tracking overview with individuals colored by group membership. B) The island in the Changuinola river (Isla Changuinola) shown with three individuals from group 3 on 2016-03-04, and C) the pairwise distances between these three individuals across that night.

Behavior & foraging patch use

Bats 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 2). 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 balsa trees in each of them. There were no flowering balsa 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. 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, glmm likelihood ratio X^2_1 = 6.861, p = 0.009; 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).

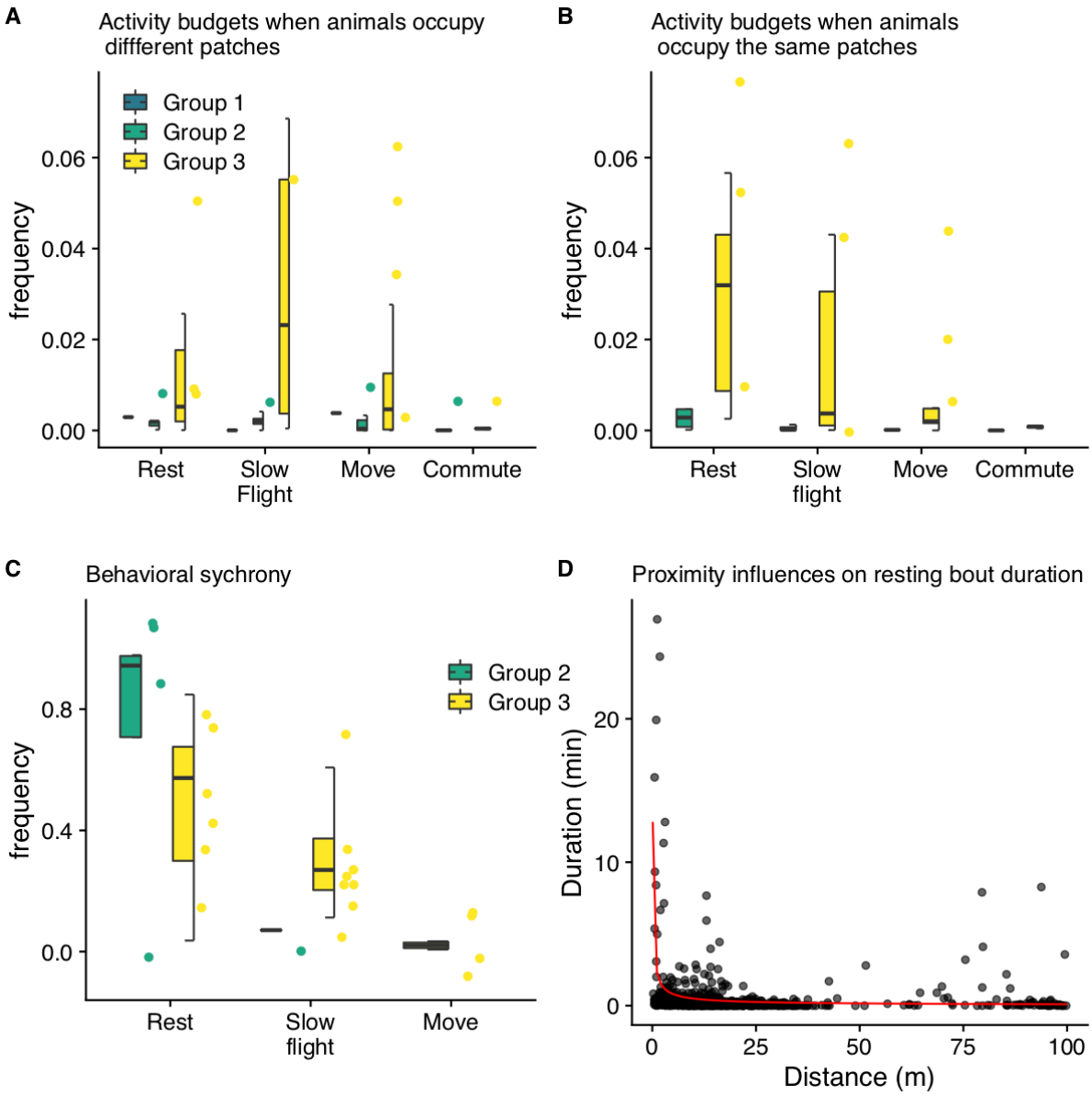

Figure 2. Effects of proximity on bat activity budgets. A) Bat activity budgets when animals occupied different patches, and B) when they occupied the same patch. C) the frequency of observations of synchronized behavior when bats occupied the same patch. Note that Group 1 members never occupied the same patch together. D) Duration of continuous resting bouts relative to the distance to a bat's nearest neighbor.

Bat activity budgets differed depending on whether they were in the same patch as their neighbors or not (Fig 2A-B), and when in the same patch bats were 24.3 ± 21.4 m apart (0.25 – 133 m), and bats in the same foraging area (e.g., Isla Changuinola) were 142 ± 70.7 m from one another (range: 1.66 – 500 m). When bats occupied the same patch, there was little synchronization in foraging behaviors, but bats were more likely to simultaneously rest than engage in other behaviors (X^2_1 = 5.5396, p = 0.018, Fig 2C). When bats occupied the same patch there was an increase in overall resting behavior and a decrease in slow flight, compared to when bats occupied different patches. 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 = 2.52 ± 0.22 m SE, $p < 0.001$, Fig 2D).

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 and number of connections was variable among groups (Fig S4). The strength of bat network connections was positively associated with the proportion of time spent in rest (Estimate: 0.769± 0.363, X^2_1 = 4.48, p = 0.034; Fig 3), and negatively associated with the proportion of time moving (Estimate: -1.129 ± 0.526, X^2_1 = 4.600, p = 0.0320; Fig 3).

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, and some individuals did not share space with any other tracked bats (Fig S4).

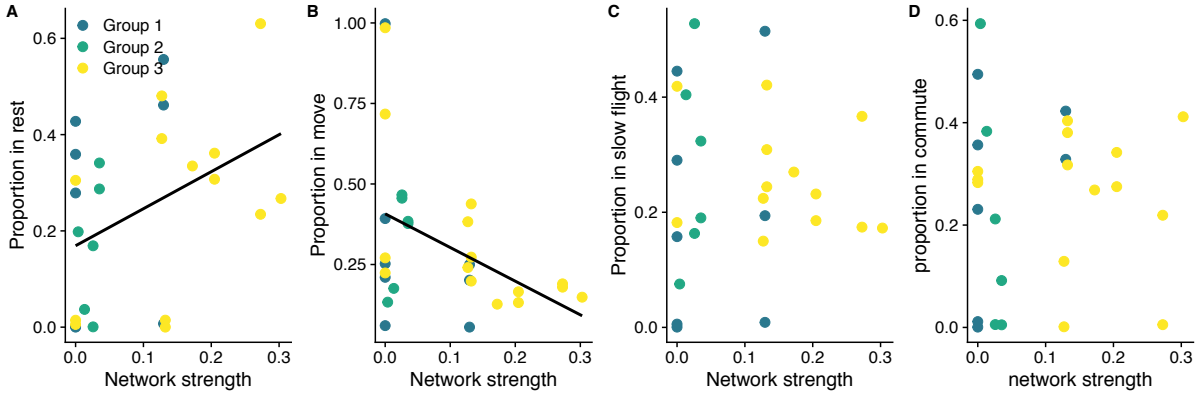

Figure 3. Relationships between proximity network strength of individual bats and the proportion of time that they spend per night A) Resting, B) Moving between patch, C) slow foraging and feeding flight, and D) Commuting.

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 the amount of time they spent outside the roost per night (Estimate: 0.760 ± 0.169, X^2_1 = 20.139, $p < 0.001$, R^2_m = 0.757, R^2_c = 0.900, 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 red in Fig 4A). To fill energetic needs incurred by longer foraging flights, bats fed from an increasing number of flower clusters (Estimate = 2.028 ± 0.430, X^2_1 = 22.22, $p < 0.001$, R^2_m = 0.372, R^2_c = 0.783, Fig 4B). Social network strength had no relationship with energy expenditure (Fig 4C), but was positively related to the amount of time that bats were tracked outside of their roost per night (Estimate: 299.66 ± 112.84, X^2_1 = 7.052, p = 0.008, R^2_m = 0.195, R^2_c = 0.467, Fig 4D). Energy expenditure, as measured through movement, more strongly depended on the total time tracked per night than on the spatial relationships among individuals in the same group.

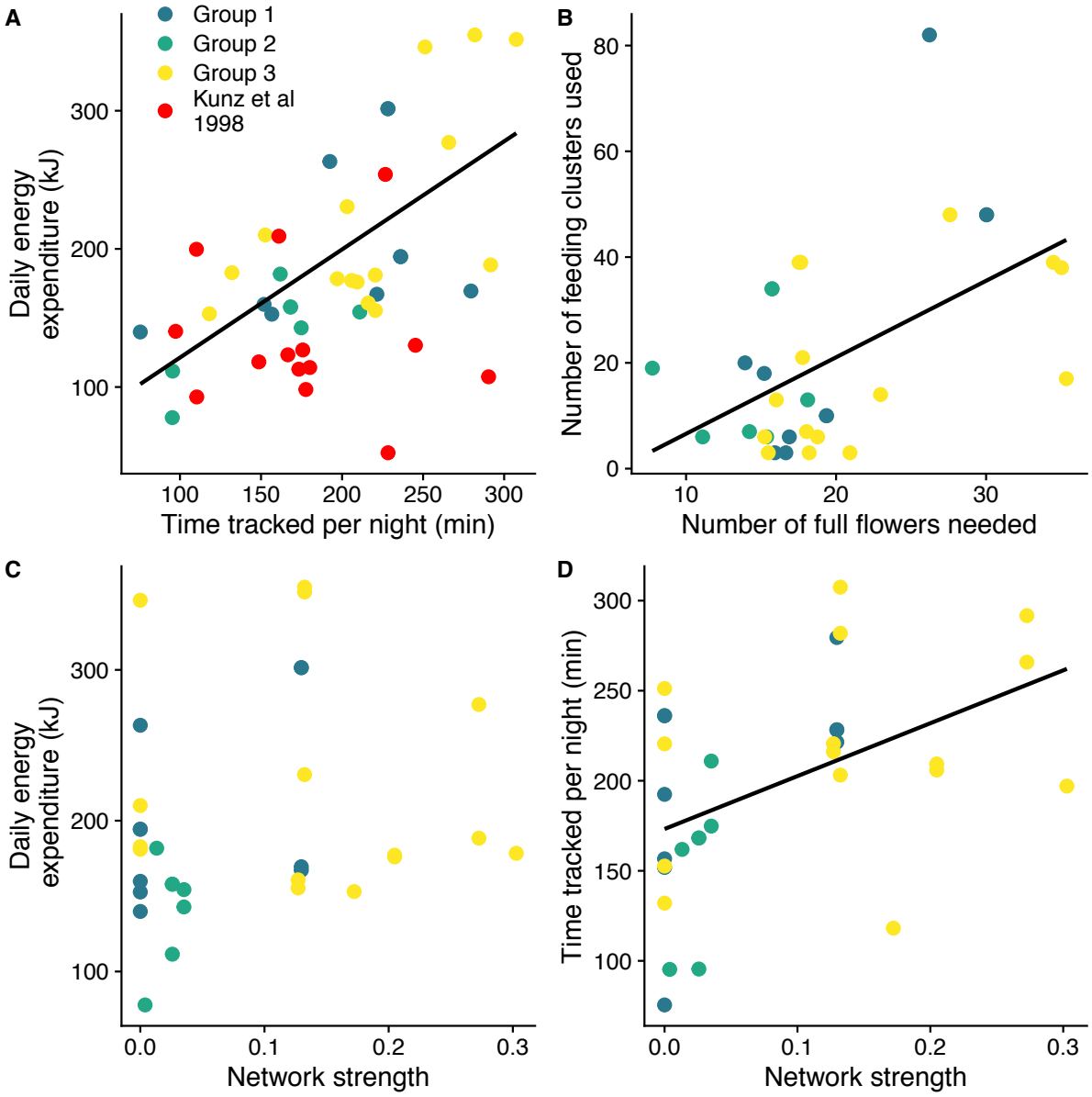

Figure 4. Estimated daily energy expenditure and the foraging returns to this DEE. A) Daily energy expenditure relative to the amount of time the bat was out of the cave, with comparative data from (Kunz et al., 1998). The line shows the relationship derived from the bats tracked in this study. B) The number of flowers needed based on average energy content to support the energy requirements of bats predict the number of feeding clusters used. C) Social network strength does not predict daily energy expenditure, but D) increases with the amount of time tracked 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 balsa flowers. While tracked

individuals did use the same foraging areas, most bats flew to these foraging patches alone instead of commuting with group mates. When bats were near group members, they tended to rest, and the close proximity of those group mates increased the duration of resting bouts. 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 *P. hastatus* across social groups used the same patches of balsa, but arrived alone. 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. During the dry season, when balsa trees flower, groups were more likely to depart together, and females from the same social group were captured around a balsa feeding site more often than randomly expected (Wilkinson and Boughman, 1998). There also appears to be strong social attraction among *P. hastatus* social groups. Social calls broadcast at flowering balsas attract 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 form strong resting associations found while outside of their roost.

It is possible that at this time of year or within this population 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 balsa flowers (Kays et al., 2012). A flowering balsa 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 balsa crown could support the daily energy needs of 3 - 7 bats. Such a limited resource may be worth defense 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. Nectar and fruit-feeding fruit bats appear to have large and robust cognitive maps of their ranges (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).

The opposite seems to be the case for social groups of *P. hastatus.* Bats commuted separately, but then foraged on different patches in the same foraging area. *Phyllostomus hastatus* were previously found to forage within 10 km of their roosts (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 balsa, where on their home island and other nearby mainland locations balsa was not yet available. This far-removed distance suggests that once a balsa 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 balsa 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.

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References

Barocas, A., Ilany, A., Koren, L., Kam, M. and Geffen, E. (2011). Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS One* **6**, e22375.

Bartoń, K. (2016). MuMIn: Multi-Model Inference, vol. R package version 1.15.6.

Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* **67**, 1-48.

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

Bell, W. J. (1990). Searching Behaviour: The behavioural ecology of finding resources. London: Chapman and Hall.

Berdahl, A., Torney, C., Ioannou, C., Faria, J. and Couzin, I. (2013). Emergent sensing of complex environments by mobile animal groups. *Science* **339**, 574-6.

Bhattacharya, K. and Vicsek, T. (2014). Collective foraging in heterogeneous landscapes. *J R Soc Interface* **11**, 20140674.

Bohn, K. M., Moss, C. F. and Wilkinson, G. S. (2009). Pup guarding by greater spear-nosed bats. *Behav Ecol Sociobiol* **63**, 1693-1703.

Bohn, K. M., Wilkinson, G. S. and Moss, C. F. (2007). Discrimination of infant isolation calls by female greater spear-nosed bats, *Phyllostomus hastatus*. *Anim Behav* **73**, 423-432.

Boughman, J. W. (1997). Greater spear-nosed bats give group-distinctive calls. *Behav Ecol Sociobiol* **40**, 61-70.

Calderón-Capote, M. C., Dechmann, D. K. N., Fahr, J., Wikelski, M., Kays, R. and O'Mara, M. T. (2020). Foraging movements are density-independent among straw-coloured fruit bats. *R Soc Open Sci* **7**.

Cameron, E. Z., Setsaas, T. H. and Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proc Natl Acad Sci U S A* **106**, 13850-3.

Clauset, A., Newman, M. E. and Moore, C. (2004). Finding community structure in very large networks. *Phys Rev E Stat Nonlin Soft Matter Phys* **70**, 066111.

Conradt, L. and Roper, T. J. (2005). Consensus decision making in animals. *Trends Ecol Evol* **20**, 449-456.

Dechmann, D., Heucke, S., Giuggioli, L., Safi, K., Voigt, C. and Wikelski, M. (2009). Experimental evidence for group hunting via eavesdropping in echolocating bats. *Proc R Soc B* **276**, 2721-2728.

Dechmann, D., Kranstauber, B., Gibbs, D. and Wikelski, M. (2010). Group hunting-a reason for sociality in molossid bats? *PLoS One* **5**, e9012.

Egert-Berg, K., Hurme, E. R., Greif, S., Goldstein, A., Harten, L., Herrera, M. L., Flores-Martinez, J. J., Valdes, A. T., Johnston, D. S., Eitan, O. et al. (2018). Resource ephemerality drives social foraging in bats. *Curr Biol* **28**, 3667-3673.

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods Ecol Evol* **4**, 1187-1194.

Fenton, M. B. (2003). Eavesdropping on the echolocation and social calls of bats. *Mammal Rev* **33**, 193-204.

Frere, C. H., Krutzen, M., Mann, J., Connor, R. C., Bejder, L. and Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proc Natl Acad Sci USA* **107**, 19949-54.

Giraldeau, L. and 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, R. A., Emek, Y., Korman, A. et al. (2020). Reinforcement learning enables resource partitioning in foraging bats. *Curr Biol*.

Hahsler, M. and Piekenbrock. (2017). dbscan: Density Based Clustering of Applications with Noise (DBSCAN) and Related Algorithms.

Harten, L., Katz, A., Goldshtein, A., Handel, M. and Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. *Science* **369**, 194-197.

Hennig, c. (2020). fpc: Flexible Procedures for Clustering.

Kays, R., Rodríguez, M., Valencia, L. and Horan…, R. (2012). Animal visitation and pollination of flowering balsa trees (*Ochroma pyramidale*) in Panama. *Mesoamericana* **16**, 54-70.

Kern, J. M. and Radford, A. N. (2021). Strongly bonded individuals prefer to forage together in cooperatively breeding dwarf mongoose groups. *Behav Ecol Sociobiol* **75**.

Kranstauber, B., Kays, R., Lapoint, S., Wikelski, M. and Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *J Anim Ecol* **81**, 738-46.

Kunz, T. H., Robson, S. K. and Nagy, K. A. (1998). Economy of harem maintenance in the greater spear-nosed bat, *Phyllostomus hastatus*. *J Mammal*, 631-642.

Liu, W., Winfield, A., Sa, J., Chen, J. and Dou, L. (2007). Strategies for Energy Optimisation in a Swarm of Foraging Robots. In *Swarm Robotics*, pp. 14-26.

McClintock, B. T., Michelot, T. and Goslee, S. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol Evol* **9**, 1518-1530.

McCracken, G. F. and Bradbury, J. W. (1981). Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behav Ecol Sociobiol* **8**, 11-34.

McInnes, A. M., McGeorge, C., Ginsberg, S., Pichegru, L. and Pistorius, P. A. (2017). Group foraging increases foraging efficiency in a piscivorous diver, the African penguin. *R Soc Open Sci* **4**, 170918.

McNab, B. K. (1969). The economics of temperature regulation in neotropical bats. *Comp Biochem Physiol* **31**, 227-268.

Michelot, T., Langrock, R., Bestley, S., Jonsen, I. D., Photopoulou, T. and Patterson, T. A. (2017). Estimation and simulation of foraging trips in land-based marine predators. *Ecol* **98**, 1932-1944.

O'Mara, M., Dechmann, D. and Page, R. (2014a). Frugivorous bats evaluate the quality of social information when choosing novel foods. *Behavioral Ecology* **25**, 1233-1239.

O'Mara, M. T., Amorim, F., Scacco, M., McCracken, G. F., Safi, K., Mata, V., Tome, R., Swartz, S., Wikelski, M., Beja, P. et al. (2021). Bats use topography and nocturnal updrafts to fly high and fast. *Curr Biol* **31**, 1311-1316 e4.

O'Mara, M. T., Scharf, A. K., Fahr, J., Abedi-Lartey, M., Wikelski, M., Dechmann, D. K. N. and Safi, K. (2019). Overall dynamic body acceleration in straw-colored fruit bats increases in headwinds but not with airspeed. *Front Ecol Evol* **7**, 200.

O'Mara, M. T., Wikelski, M. and Dechmann, D. K. N. (2014b). 50 years of bat tracking: device attachment and future directions. *Methods Ecol Evol* **5**, 311-319.

O'Mara, M. T., Wikelski, M., Voigt, C. C., Ter Maat, A., Pollock, H. S., Burness, G., Desantis, L. M. and Dechmann, D. K. (2017). Cyclic bouts of extreme bradycardia counteract the high metabolism of frugivorous bats. *eLife* **6**, e26686.

Page, R. and Ryan, M. (2006). Social transmission of novel foraging behavior in bats: frog calls and their referents. *Curr Biol* **16**, 1201-1205.

Pennycuick, C. J. (2008). Modelling the flying bird. London: Academic Press.

R Core Team. (2020). R: A language and environment for statistical computing: R Foundation for Statistical Computing, Vienna Austria.

Ramakers, J. J. C., Dechmann, D. K. N., Page, R. A. and O'Mara, M. T. (2016). Frugivorous bats prefer information from novel social partners. *Anim Behav* **116**, 83-87.

Ranacher, P., Brunauer, R., Trutschnig, W., Van der Spek, S. and Reich, S. (2016). Why GPS makes distances bigger than they are. *Int J Geogr Inf Sci* **30**, 316-333.

Ratcliffe, J. and ter Hofstede, H. (2005). Roosts as information centres: social learning of food preferences in bats. *Biol Lett* **1**, 72-74.

Riehl, C. and Strong, M. J. (2018). Stable social relationships between unrelated females increase individual fitness in a cooperative bird. *Proc R Soc B* **285**.

Robitaille, A. L., Webber, Q. M. R., Vander Wal, E. and Golding, N. (2019). Conducting social network analysis with animal telemetry data: Applications and methods using spatsoc. *Methods Ecol Evol* **10**, 1203-1211.

Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., Cruz, S., Proano, C., Takekawa, J. Y., Newman, S. H. et al. (2013). Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. *Mov Ecol* **1**, 4.

Samuni, L., Crockford, C. and Wittig, R. M. (2021). Group-level cooperation in chimpanzees is shaped by strong social ties. *Nat Commun* **12**, 539.

Schubert, E., Sander, J., Ester, M., Kriegel, H. P. and Xu, X. (2017). DBSCAN Revisited, Revisited. *ACM Transactions on Database Systems* **42**, 1-21.

Schülke, O., Bhagavatula, J., Vigilant, L. and Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Curr Biol* **20**, 2207-10.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philos Trans R Soc B* **362**, 539-59.

Silk, J. B., Alberts, S. C. and Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science* **302**, 1231-1234.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. and Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Curr Biol* **20**, 1359-61.

Snijders, L., Krause, S., Tump, A. N., Breuker, M., Ortiz, C., Rizzi, S., Ramnarine, I. W., Krause, J. and Kurvers, R. (2021). Causal evidence for the adaptive benefits of social foraging in the wild. *Commun Biol* **4**, 94.

Speakman, J. (2005). Body size, energy metabolism and lifespan. *Journal of Experimental Biology* **208**, 1717-30.

Stern, A. A. and Kunz, T. H. (1998). Intraspecific variation in postnatal growth in the greater spear-nosed bat. *J Mammal* **79**, 755.

Thomas, S. P. (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. and Nathan, R. (2020). Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system. *Science* **369**, 188-193.

Valone, T. J. (1989). Group foraging, public information, and patch estimation. *Oikos*, 357-363.

von Busse, R., Swartz, S. M. and Voigt, C. C. (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**, 2073-80.

Ward, S., Moller, U., Rayner, J. M., Jackson, D. M., Bilo, D., Nachtigall, W. and Speakman, J. R. (2001). Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris*. *J Exp Biol* **204**, 3311-22.

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

Wilkinson, G. S. (1986). Social grooming in the common vampire bat, *Desmodus rotundus*. *Anim Behav* **34**, 1880-1889.

Wilkinson, G. S., Carter, G. G., Bohn, K. M. and Adams, D. M. (2016). Non-kin cooperation in bats. *Philos Trans R Soc B* **371**.

William, T. C. and Williams, J. M. (1970). Radio tracking of homing and feeding flights of a neotropical bat, *Phyllostomus hastatus*. *Anim Behav* **18**, 302-309.

Wright, G. S. (2016). Social Learning and Information Transfer in Bats: Conspecific Influence Regarding Roosts, Calls, and Food. In *Sociality in Bats*, (ed. J. Ortega), pp. 211-230: Springer.

Wyman, M. T., Pinter-Wollman, N., Mooring, M. S. and Hayes, L. (2021). Trade-offs between fighting and breeding: a social network analysis of bison male interactions. *J Mammal*.

Supplemental Information

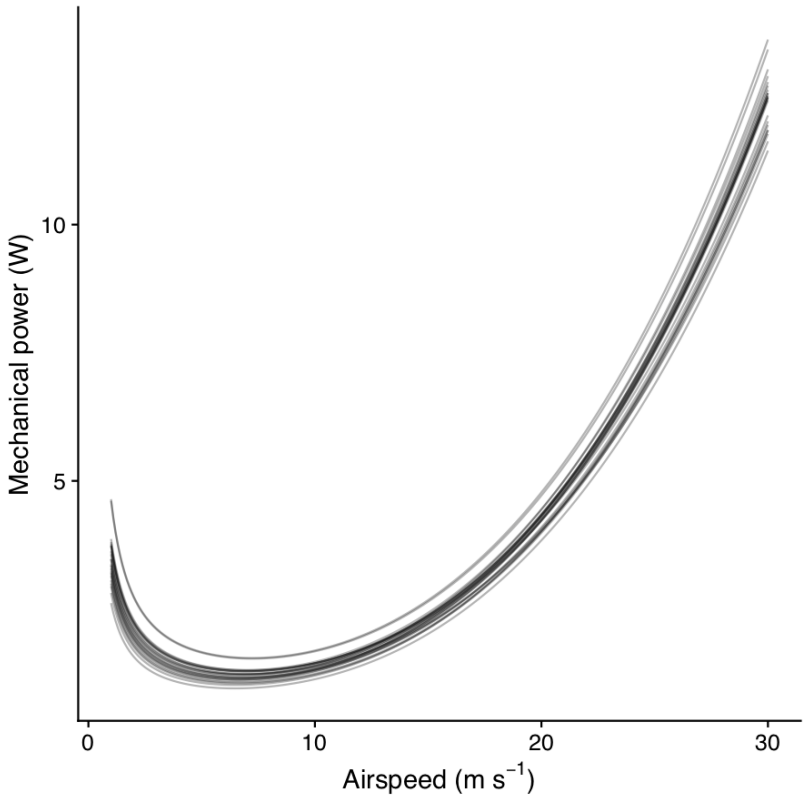

Figure S1. Mechanical power requirements at airspeeds for each bat in this study. Power output was calculated following Pennycuick (2008) at 50 m and 25°C using each individual's body mass and wing dimensions.

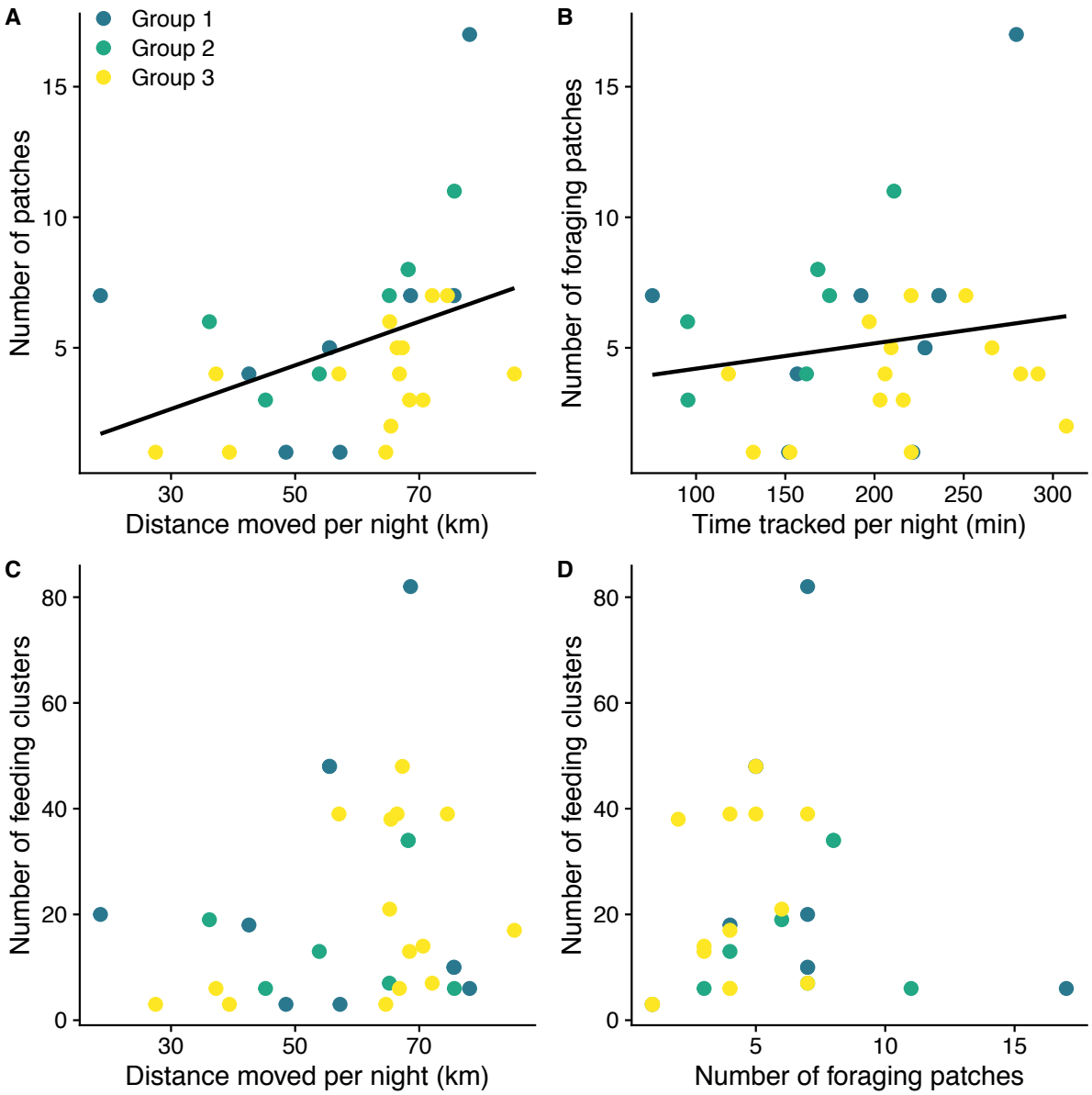

Figure S2. The number of foraging patches used is predicted by A) the distance that individuals moved each night and B) the total time that individuals were tracked each night. The number of feeding clusters identified was not predicted by either C) the distance moved per night or D) the number of foraging patches used.

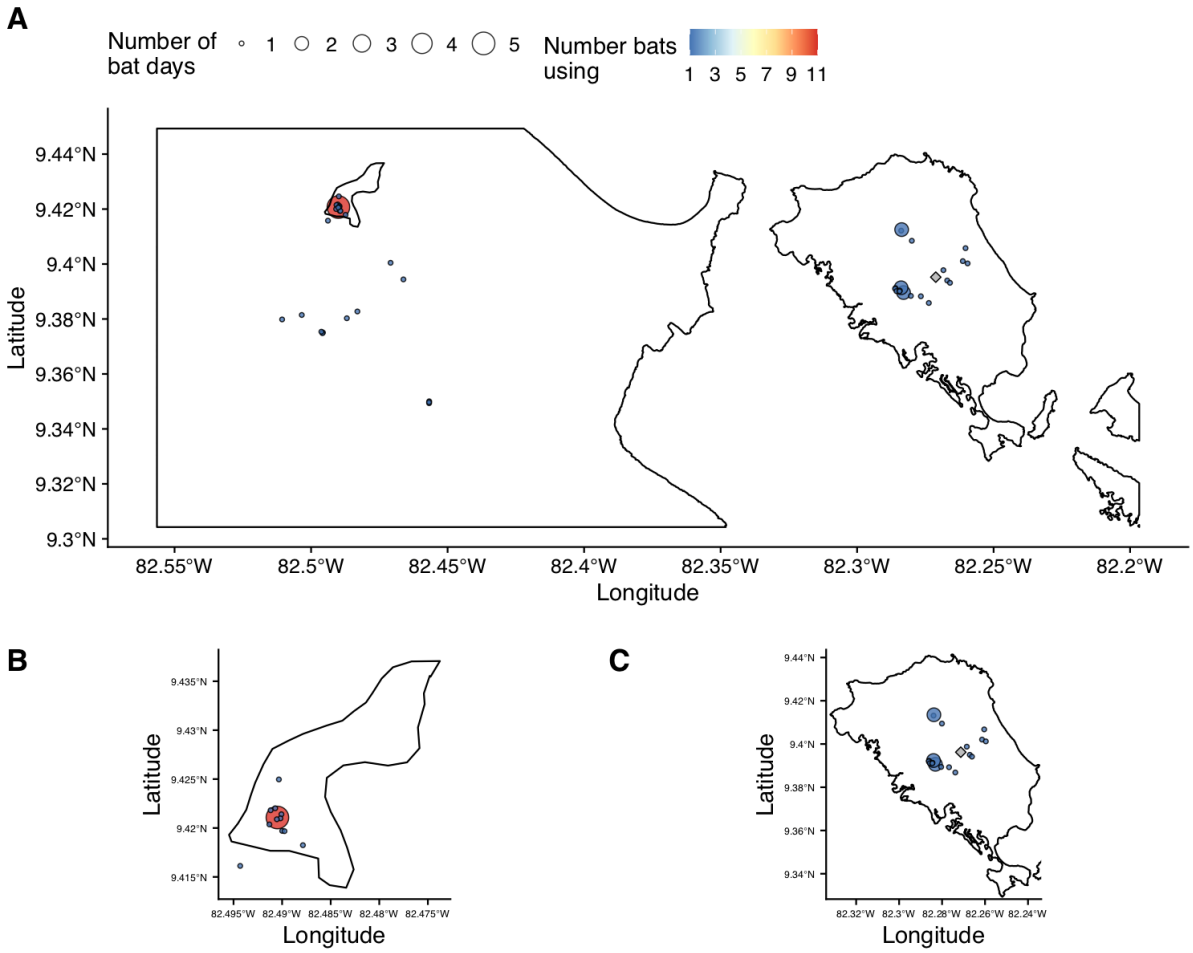

Figure S3. Resting patches clustered from GPS locations. A) Resting patches are shown across the study area, scaled by the number of individual bat days that the sites were used and colored by the number of individual bats that used the patch. Resting patches are shown for B) Isla Changuinola, and C)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

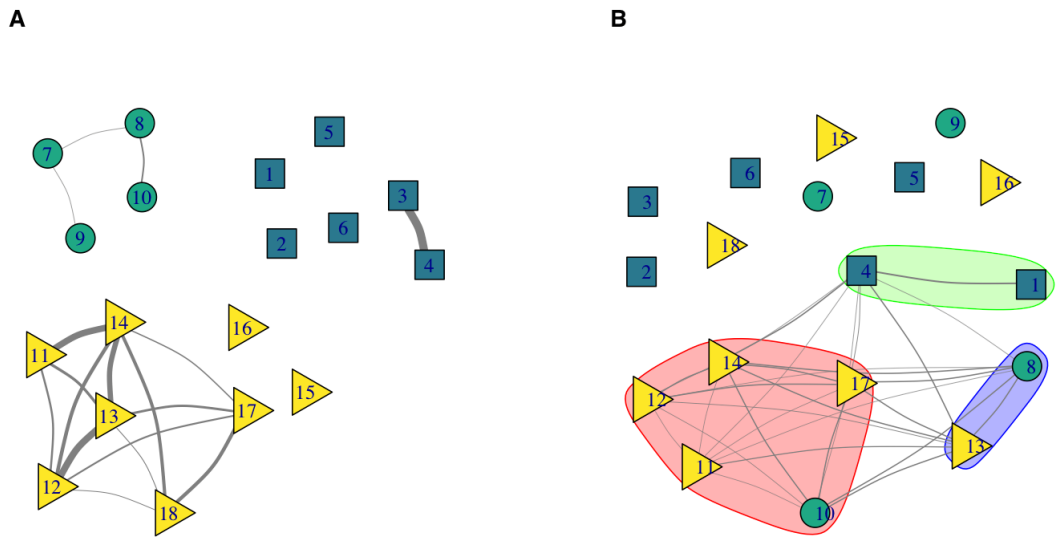

Figure S4. A) Proximity networks of simultaneous spatial associations (same space, same time); B) networks of across-night foraging patch associations (same space, different time). Individual bats are shown as part of their social group (group 1: blue square, group 2: green circle, group 3: yellow triangle.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