

Foraging and commuting habitats of the greater horseshoe bat, revealed by high-resolution GPS-tracking

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Abstract

Background Echolocating bats make a series of decisions to select their flight routes based on auditory information obtained by sonar; accumulations of these flight routes are represented as daily movement patterns. However, there is still a lack of a unified understanding of continuous movements of echolocating bats in the wild from small to large spatial scales (i.e., from meters to tens of kilometers). In this study, we investigated nightly flight paths of the Japanese greater horseshoe bat, *Rhinolophus ferrumequinum nippon*, using high-resolution GPS data loggers. Our aim was to identify foraging and commuting behavior based on the observed movement patterns and to investigate the relationship between these movement types and specific habitats.

Results We found that the majority of tagged bats alternated between foraging and commuting behavior throughout the tracking period, and one individual moved 23.6 km from its roost. The bats usually left a stay point in the opposite direction from which they entered it, indicating that almost all of the stay sites were on their way to another destination. The distance between two successive foraging sites was on average 332 ± 398 m (mean \pm standard deviation), and half of all foraging periods lasted less than 3 min. An analysis of habitat use revealed that the bats used conifer plantation and natural forests as pathways and feeding habitats.

Conclusions Our findings suggest that the structure of the forests have a great influence on the nocturnal behavior of the greater horseshoe bats. Although this study has a descriptive character due to a relatively small number of tagged individuals, it was possible to elucidate the small-scale interactions between wild *Rhinolophus* bats and their environment using the latest high-resolution GPS technology, which will allow us to give new insights into the foraging ecology of echolocating bats in the wild.

Background

Animals choose a route towards a destination based on their innate sensing systems and behavioral strategies [1, 2]. Most bat species, except for a part of Pteropodidae, select flight routes based on information obtained by echolocation [3]. Since their echolocation calls do not propagate usually over large distances in the air (< 10 m [4]), most studies have focused on small-scale relationships between bat echolocation and flight routes in the laboratory and small-scale field experiments [5–9]. Recently, technological advances in the design of animal-borne devices have opened new avenues for research of bat navigation on a much larger spatial scale. Bio-logging (i.e. storing data within tags) has facilitated data collection of large-scale movement paths [10], and also accelerated the investigation of movement ecology of echolocating bats in the wild. Previous studies indicate that a state-switch between the two behavioral modes of commuting and foraging is the most basic behavior of bats, as shown in other animal species [11]. For example, a GPS tracking study revealed that the flight patterns of *Myotis* bats are associated with the predictability of prey occurrence [12]; the mouse-eared gleaning bat, *Myotis myotis*, commutes to a particular foraging site with a predictable occurrence of prey in a straight line, whereas the Mexican fish-eating bat, *M. vivesi*, wanders over the ocean to search for ephemeral resources and exhibits

intensive movement patterns in a local area while foraging. However, there is still a lack of a unified understanding of continuous movements between the commuting and foraging of echolocating bats in the wild due to the long-time sampling intervals. As bats maneuver so adeptly that they could fly about several meters per second, more precise recording is needed.

The greater horseshoe bat (*Rhinolophus ferrumequinum*) is a good model to investigate the relationship between the foraging and commuting flight mode, as it is known to forage in the fly-catcher style (i.e. bats hang on a tree branch to search prey insects and then fly off to capture it) [13, 14], which may cause two distinct flight patterns: foraging and commuting. Regarding movement ecology during natural foraging, many studies have been conducted in the greater horseshoe bat using radio-tracking [e.g., 15–20], and in recent years GPS-tracking [21]. According to these studies, the greater horseshoe bats preferred a particular habitat type during foraging (pasture, forest, riparian vegetation, etc.). In addition, they moved on average relatively short distances of a few kilometers during nightly foraging. However, the basic flight properties of the commuting and foraging behavior and how environmental features shape these movement patterns among flight modes still remain unknown because the accuracy and frequency of the positional measurements using radio-tracking and low-frequency-sampling GPS-tracking [21] were not sufficient to identify the habitat type of the immediate surrounding of the bat during the flight.

The purpose of this study is firstly to precisely distinguish between the commuting and foraging mode based on the flight paths during natural foraging. In a second step, we aim at describing the spatio-temporal characteristics of each flight mode. To address this purpose, we mainly used high-resolution GPS positions (i.e. logging every 2–3 s) for the Japanese greater horseshoe bat (*Rhinolophus ferrumequinum nippon*) during nightly foraging. We hypothesized that the bats show alternating patterns of foraging and commuting, and navigate themselves to a habitat that is suitable for their fly-catcher foraging style. The investigation of the small-scale as well as the nocturnal movement behavior using high-resolution GPS-tracking will make it possible to support previous findings based on more concrete evidence and will contribute to dramatic progress in the understanding of the movement ecology of this bat species.

Results

Overview

Two types of GPS data loggers, GiPSy-5 (2–3 sec interval logging for 4 h) and PinPoint-50 (600 sec interval logging for 9 h), were used in this study and either of the two was attached to a total of 27 bats (GiPSy-5, 24; PinPoint-50, 3). We collected data from a total of seven loggers (GiPSy-5, 5; PinPoint-50, 2; Table 1) out of ten tagged bats that returned to the roost (i.e., three loggers were dropped elsewhere). In general, bats flew towards the northwest (Fig. 1A). Most bats with attached loggers left the roost (i.e. logging started) within about 1 h after sunset, which was similar to previously reported bat emergence times (Table 1) [14]. Two bats with PinPoint-50 were both not located for short period but almost continuously logged during midnight after starting to log position, and then not logged until the time of

sunrise over an hour (see Additional file 1 in detail). We observed foraging trajectory patterns (Fig. 1BC) among the flight paths of all bats. One of the seven bats remained at a single location for over 4 h (bat D); another flew away from a stay site and returned repeatedly to that site (bat C₂, Fig. 1C) in a foray search pattern [22, 23]. Although bat D was caught in a drizzling rain for approximately 1 h around 23:00, the weather was clear or cloudy during all other measurement periods (Japan Meteorological Agency, www.jma.go.jp).

Properties of each mode

Since the bats were expected to forage at a stay site, we identified and focused on the foraging and commuting modes, analyzing these in detail using the clustering method that we proposed in this study (see Methods for details). All bats, except bat C₁, spent more than 70% of their time staying at different sites. bat C₁ flew relatively long distances interrupted by short stays (28% of all bat C₁'s positions) and flew almost directly towards the northwest over a distance of 23.6 km, which was the longest flight distance recorded in this study.

The bats repeatedly switched between foraging and commuting modes. They usually left a stay point in the opposite direction from which they entered it (Fig. 2A), indicating that almost all of the stay sites were on their way to another destination. We recorded a maximum of 42 stays for a single bat (average: one 5–6-min stay; Table 1), which did not overlap between recorded flight trajectories. The majority of stationary periods lasted for less than two minutes, and half of all stays lasted less than three min (Fig. 2B). Most of the stay sites were located close to each other with an average distance of 332 ± 398 m (mean \pm SD, N = 87) and a maximum travel distance of approximately 2.8 km and a negative exponential distribution (Fig. 2C).

Habitat use

We examined the habitat use of bats for foraging- and commuting-mode behavior. In this study, the habitats were categorized into the following six groups: natural forest, grassland, urban area, conifer plantation, water and cropland (Fig. 3A). The urban area is widely distributed on the south side of the roost. The bats flew mainly toward natural forests. All of the habitats during the foraging-mode (white circles in Fig. 3A) were either natural forest (73.4%) or conifer plantation (26.6%) (Fig. 3B). Similarly, almost all habitats during the commuting-mode were also forested area (75% and 22% for natural forest and conifer plantation respectively, Fig. 3C). Also bat A and B that logged by PinPoint-50, over 95% of measured positions belonged to the natural forest or conifer plantation. These results indicate that the main habitat where the bats used during nightly natural foraging was forested area.

The GPS loggers used in this study recorded also data on the altitude, although not at high accuracy. Bat ground height during commuting mode was 16 ± 20 m (mean \pm SD, N = 5456), whereas the height of the stationary logger that we placed 1 m above the ground in the forest was 8 ± 12 m (mean \pm SD, N = 985), indicating that bat flight altitude was less than 10 m on average. The forest canopy heights in the study

area have been reported as approximately 15–20 m [24, 25]. These findings indicate that bats flew mainly within or under the forest canopy, not above it.

Discussion

Using bat flight trajectories recorded by GPS loggers, we developed a method to discriminate between foraging and commuting modes, such that we were able to quantify spatio-temporal features of these two navigational modes in *R. f. nippon*. Thus, it is possible to use our method to estimate phases of large-scale navigation among echolocating bats, i.e. foraging or commuting during nightly movement, based on the flight path. As a result, we first demonstrated that *R. f. nippon* alternated foraging within a time frame of a few minutes, which is quite similar to the Area Restricted Search (ARS) behavior observed in the movement patterns of animals such as some mammals, birds, and insects [26–28]. In addition, the full-night GPS tracking using pinpoint-50 showed that bats moved out of the roost at midnight while there were times when they could not be recorded. Such activity is consistent with the previous study on the usage of the night roost (i.e., a roost for resting) by the Japanese greater horseshoe bat [14]. These kinds of characteristics of foraging and commuting behavior should be investigated in the future because the sample size in the present study was small. We are confident however that it will provide very valuable knowledge in order to advance the understanding of foraging ecology of this bat species in the wild.

Habitat use

We also verified the habitat use of *R. f. nippon* during nightly foraging activity with fine resolution after dividing the whole measured path into commuting and the foraging modes. The main habitat used in both of the movement modes were forested areas, and the bats seemed to prefer flying within forest (see Fig. 3). Several factors may cause this habitat usage for the bats in our study area. First, forests are suitable for the flycatcher feeding style due to the abundance of tree branches. Second, *Rhinolophus* species generally have lower wing loading, which results in slow flight and good maneuverability [29]; flying within forests allows bats to avoid harsh weather conditions. Third, forests are a major source of flying insects, which are consumed by insectivorous bats. In a previous study conducted in the UK using radio telemetry, *R. ferrumequinum* preferred to fly over pastures and in forests [19, 30], whereas the bats in western Europe preferred residential areas and meadow orchards [20]. Our present data show that pastures, meadows, orchards (categorized into grassland in this study) and residential areas were rarely used by the bats. The reason of such difference in the habitat use of each population is unknown. Feeding style might be slightly different between the populations, or the environmental factors, such as landscape structure and available prey abundance in each habitat might affect habitat use. The landscape in this study was largely covered by forests than the landscapes in those previous studies. In the future, larger sample size and comparative study will be necessary to understand the habitat preference of this bat species.

In the forest, the bats often commuted along a road (Fig. 4). The forest road provided a sufficiently wide and open space for a car to pass through (Additional file 2), and bats flew along this road (asterisk in

Fig. 4). Based on direct visual observation or infrared camera recordings in small-scale areas it has been demonstrated that bats fly along fixed routes, so-called flyways, when commuting to foraging sites [31–33]. Such a route-following behavior is one of the various large-scale navigation strategies of bats that have been previously reported [34], and bats are thought to use forest roads as navigation cues. Furthermore, the ultrasound detection range of bats is shorter than the ranges of visual sensory systems employed by other animals such as birds. Thus, when moving along a road that can be detected by receiving echoes from the ground and tree lines on the left/right side, bats may not only move easily and quickly, but these cues may also help in creating local spatial maps that could be accumulated for large-scale movement.

Case study

We recorded two cases of unrepeated commuting and foraging (bats C_1 and D). For bat C_1 , the foraging time during one trip was relatively short and flight speed was clearly higher compared to those of other trips, even by the same individual (see Table 1). These data suggest that on that day, this bat flew with a goal other than foraging. Note that bat C_1 might have flown at a higher speed than the other due to the wind effect: bat C_1 received approximately 2 m/s wind from south, bat C_2 received 1 m/s wind from west and bat E, F and G received 3–4 m/s wind from north (Japan Meteorological Agency, www.data.jma.go.jp). Previous studies have reported that many insectivorous bat species, such as *Myotis* and *Plecotus* species, travel considerable distances and swarm at underground sites in late summer and autumn in temperate regions [35–37] for mating [38, 39] and/or to assess potential hibernation sites. Although there is no evidence of swarming behavior by *Rhinolophus* species so far, it is possible that bat C_1 has traveled a long distance because of an unknown social behavior during the mating season.

In contrast, bat D stayed continuously at a single site near the roost for over 4 h early in the night (Fig. 1C) (note that we visited this site and found that this was an area next to a pond, with a relatively low tree density). The positions of bat D had a Gaussian distribution in both the north-south and east-west directions (Additional file 3), with a greater variation along the north-south axis compared to the variation from our error-measurement when the logger was placed in a single location within the forest (Additional file 4, see Methods for details). This result suggests that these data were not the result of GPS logging error but rather a result of bat movements within the stay site near their roost. Note that, the bat's position located discretely by GPS during the foraging mode should not appear to move because the fly-catching greater horseshoe bats fly back to the position where they perched before attacking insect [14]. Therefore, basically, it is thought to be hard to discriminate foraging or not (i.e., resting) from the foraging-mode trajectory data. In the case of bat D, the stay period was enormously longer than the other stays identified in this study. This bat might repeatedly change the hunting site in the nearby area in the long-time foraging.

Ethical considerations

As bio-logging studies of wild echolocating bats have recently flourished, data quality is likely to be prioritized under a trade-off between logger size and battery life, resulting in the use of data logger weighted more than 10% of the body mass [40, 41]. In this study, we limited the logger weight to be relatively small, i.e., less than 10% of the bat's body mass, although the logger weight is recommended to be less than 3–5% of the body mass for the flying animals such as birds [42] and bats [43]. A previous study showed that no significant differences were observed between the behavior of echolocating bats (*M. myotis* and *M. vives*) carrying loggers with 15% of their body weight and non-tagged individuals [12]. The results of the present study showed that bats flew long distances at almost the same speed as reported by previous studies using radio telemetry [44, 45], suggesting that the influence of the data logger weight on bat flight performance was negligible. Nevertheless, the data logger needs to be smaller in the future in order to minimize the effect of the extra loading.

We also should consider how the stress caused by handling and logger attachment affects the bat's movement, as it might behave or move differently than usual and/or might lose body weight. The results showed that the time when the tagged bats emerged from their roost in the present study was almost the same as in a previous study [14]. In addition, the bodyweight of the attached bats when recapturing after a couple of days did not obviously decrease compared to the first capture (see Methods for details), which is consist of the range of the bodyweight fluctuation observed in this bat species on a daily basis among the reared individuals in our laboratory. These observations suggest that the extra loading due to the logger had little effect on the habitat use of the horseshoe bats. Furthermore, we recaptured a female that was investigated in the previous year during its pregnancy and we could not find any damages. In the present investigation, we caught and attached loggers to a total of 27 bats. We only recaptured 10 bats (approximately 40% recapture rate) and succeeded in recovering the data from 7 individuals. In previous studies, the recapture rate of the greater horseshoe bats which were tagged with small metal rings (several few milli-meters) was also around 40% [14, 46]. Therefore, the low recapture rate in this study is unlikely due to the extra loading from the GPS data logger alone. However, at present, the effect of logger attachment on the recovery rate of individuals as well as local populations has not been quantitatively assessed. Therefore, detailed investigations of the effects of logger attachment on the bats' behavior and health are needed.

Conclusion

We used high-resolution GPS bio-logging data and a flight mode classification method to determine that (i) greater horseshoe bats remained within a stay area repeatedly, to a maximum of about 10 times per hour during large-scale nightly navigation, and (ii) bats mainly commute and forage in natural forests or conifer plantations, and commuted locally and reliably along a forest road. Our findings suggest that the forests and their structures have a great influence on the nocturnal behavior of the greater horseshoe bats. The results of this fine-scale bio-logging study will improve our understanding of the navigation and acoustical sensing strategies of insectivorous echolocating bats in the wild.

Methods

Bats and study site

The target species of this study was *Rhinolophus ferrumequinum nippon*, which has a body length and mass of approximately 6–8 cm and 20–30 g, respectively [47]. *R. f. nippon* starts to forage shortly after sunset and hunts flying insects mainly in a flycatcher style [13, 14]. We caught the bats using butterfly nets and then attached GPS data loggers to their backs at their day roost, an abandoned pillbox in Tomakomai, southern Hokkaido, Japan (N 42°41'00.2" E 141°40'13.1"). A forest and a golf course are located north of the roost, and an urban area lies to its south. The forests are mainly natural secondary forest dominated by *Quercus crispula* with interspersed patches of conifer plantations. Body mass was measured with an electronic scale (Handy-mini-1476, TANITA, Tokyo). All bats were tagged with numbered aluminum rings (4.2 mm, Lambournes Ltd., Leominster, England) that were attached to their forearms.

GPS tracking

The main GPS data logger that we used in this study was GiPSy-5 (Technosmart, Italy; 2.3 g), which is capable of logging position in high-resolution. Additionally, since this study is one of the very few bio-logging investigations of *R. ferrumequinum*, pinpoint-50 data logger (Biotrack, UK; 2.2 g; 0.3 g radio-transmitter unit) was probatively used to obtain a holistic view of its nightly movement behavior. The PinPoint-50 units were set to log every 600 s such that the entire flight path would be tracked during the night (approximately 9 h). In contrast, the GiPSy-5 logging interval was set to two or three seconds, for continuous logging over a period of approximately 4 h, to measure high-resolution smooth flight paths. Timers were set on both types of loggers to start logging at 19:00 o'clock. The GiPSy-5 and PinPoint-50 units were set to sleep for 15 min and output the value zero if they failed to detect satellite signals for 300 s and 70 s, respectively. We shaved dorsal hair of each bat and attached either of the two loggers using Skin Bond (Osto-bond, Montreal Ostomy Inc., Canada) during the daytime on a total of 7 days: June 2 and September 3, 2015; June 10, 11, and 12, 2016; and September 2 and 5, 2016. The weight of the attached logger was less than 10% of that of the bat and exceeded the 5% threshold of body mass commonly recommended for bats [43]. However, recent GPS studies have confirmed that bats may be able to cope with additional loads exceeding 10% of their body mass without apparent changes to foraging behavior or body mass [40, 41]. In this study, flight speeds of the bats were calculated to be similar to or greater than previously reported values [44, 45], suggesting that the influence of data logger weight on bat flight performance was negligible. The attached loggers were collected by recapture the day after attachment at the same roost. We used a remover liquid (Uni-Solve Adhesive Remover, Smith and Nephew, UK) to remove the data loggers as gently as possible from the backs of the bats. There were no distinct changes in body weight between deployment and recovery (-1 g for three bats in 2016, no data in 2015). In addition, the dorsal fur of several recaptured individuals that were tracked in the previous year fully grew back.

Data analysis

When *R. f. nippon* flies in forests, GPS measurement error may be relatively high. Therefore, we measured the position error of GiPSy-5 data loggers at three different sites in the forest near the roost, prior to data analysis. The measured positions followed a Gaussian distribution, with a peak at the center of the coordinates and a standard deviation (SD) σ of 7–8 m in the north–south and east–west direction (Additional file 4). We classified each GPS-point as belonging to the foraging or commuting behavior, including the positional error, as follows: we assigned foraging-mode behavior to any position with a maximum distance ($\max-d_{\text{window}}$) of < 50 m (about $\pm 3\sigma$) between two points logged within 30 s (15 s before and after) of the current position. Note that the 30-second time window was assumed based on the bats' flight speed and the GPS positional error. When $\max-d_{\text{window}}$ exceeded 50 m, the position would be assigned to the commuting-mode behavior. To minimize false classifications due to positional error, we used smooth processing ("smooth" function with 5-point moving average algorithm in the Matlab R2016b environment; Mathworks, USA) for the $\max-d_{\text{window}}$ time series. In rare cases, e.g. when the logger was stationary, $\max-d_{\text{window}}$ exceeded 50 m during a time window of 30 s, so that a given GPS-point was classified as belonging to the commuting mode. To correct this false classification, we reclassified any GPS-point classified as "commuting mode" to "foraging mode" when it was preceded and followed by a "foraging mode" position within an area of 50 m \times 50 m. Two bats tracked using PinPoint-50 loggers were excluded from this analysis because the trajectory was too rough (every 600 s logging). An example of the result of this procedure is provided in the Supplemental information (Additional file 5). In previous studies, first-passage time analysis and state-space analysis have been proposed for the extraction of local search paths [11, 48]. However, the method proposed in this study was developed simply by considering positional variation in GPS tracking data. We performed this analysis using a custom-made program in Matlab. The geographical information system analysis was performed using the ArcGIS Desktop 10.4 software (Esri Japan Corporation).

Abbreviations

GPS
Global positioning system,

Declarations

Ethics approval and consent to participate: Experiments were performed with permission from the Hokkaido Regional Environment Office, Ministry of the Environment Government of Japan. (2015; 21-27-0077 – 21-27-0092; 2016; 21-28-0088 – 21-28-0093).

Consent for publication: Not applicable

Availability of data and materials: Trajectory data of the bats used in this study are available in the Additional file 1.

Competing interests: The authors declare no conflict of interest.

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Author contributions: EF and SH designed the study; EF, K. Yoshimura, TU, and DF performed the experiments; EF, KY, KY, and DF analysed the data; EF, K. Yoda, DF, and SH wrote the paper. All authors gave final approval for publication.

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Tables

Table 1. Summary of bat flight data used in this study.

Bat	Sex	Logger Type	Logging Interval [s]	Measured Date	Sunset* Time	Time Log Start	Time Log End	No. Points	Ratio of Stay	No. Stays	Flight speed** (mean ± SD [m/s])	Reason of Log End
A	♂	PinPoint-50	600	2015/6/2-3	19:08	20:15	3:00	38	—	—	—	Signal lost
B	♂	PinPoint-50	600	2015/6/2-3	19:08	20:05	1:30	27	—	—	—	Signal lost
C ₁	♂	GiPSy-5	2	2015/9/4	18:07	1:37	3:50***	3536	28%	3	5.2 ± 1.9 (N = 2507)	Signal lost
C ₂	♂	GiPSy-5	2	2015/9/5	18:06	0:17	0:34	544	71%	4	4.2 ± 2.1 (N = 138)	Battery out
D	♂	GiPSy-5	2	2015/9/3	18:07	19:31	23:45	8002	100%	1	—	Battery out
E	♂	GiPSy-5	3	2016/6/10	19:13	19:32	23:42	5156	89%	27	3.8 ± 1.5 (N = 521)	Battery out
F	♂	GiPSy-5	3	2016/6/10	19:13	19:33	23:29	5298	72%	42	4.0 ± 1.7 (N = 1441)	Battery out
G	♂	GiPSy-5	3	2016/6/10	19:13	19:49	23:00	4101	80%	17	4.2 ± 2.3 (N = 803)	Battery out

* Data from National Astronomical Observatory of Japan were used.

** Each flight speed was calculated using two consecutive positions in the commuting-mode trajectory (see Additional file 5).

*** GPS signal was temporarily lost during the period between 2:01 - 2:31.

Additional Files

Additional file 1 (xlsx)

Dataset of the GPS coordinates from bats used in this study.

Additional file 2 (jpg)

Photograph taken towards north from the point indicated by the asterisk in Fig. 4. Bat F flew along this forest road.

Additional file 3 (pdf)

Positional distribution of the GPS data logger (GiPSy-5) that was attached to Bat D (Fig. 1C). The origin represents the center of 8002 measured positions. We observed Gaussian distribution in the north–south

and east–west directions. The distribution along the north–south axis was more variable than that along the east–west axis.

Additional file 4 (pdf)

Positional distribution of GPS data loggers (GiPSy-5) placed at three different sites (indicated by colored markers) within the forest near the bat roost. The origin represents the center of positional measurements at each site. A Gaussian distribution was observed the north–south and east–west directions. The total number of positions was 985: 172 for site 1 (squares), 302 for site 2 (circles), and 511 for site 3 (crosses).

Additional file 5 (pdf)

Example of commuting and foraging trajectory patterns separated using the state-estimation method. **(A)** Flight path of bat G during foraging, commuting, and returning to the foraging site. Arrows indicate flight direction. **(B–E)** State-estimated flight paths were divided into four sections: first (B), second (C), third (D), and last (E). Dark brown and beige points indicate foraging-mode and commuting-mode positions, respectively. **(F–H)** Proportional distributions of flight speed, calculated using two successive measured positions, for all positions (F), foraging-mode (G), and commuting-mode (H). Mean flight speed was calculated using commuting-mode flight speed data.

Figures



Figure 1

(A–C) Flight trajectories measured by the GPS tracking of the bats drawn on large- **(A)**, medium- **(B)**, and small-scale **(C)** satellite images. Arrows represent bat flight directions.

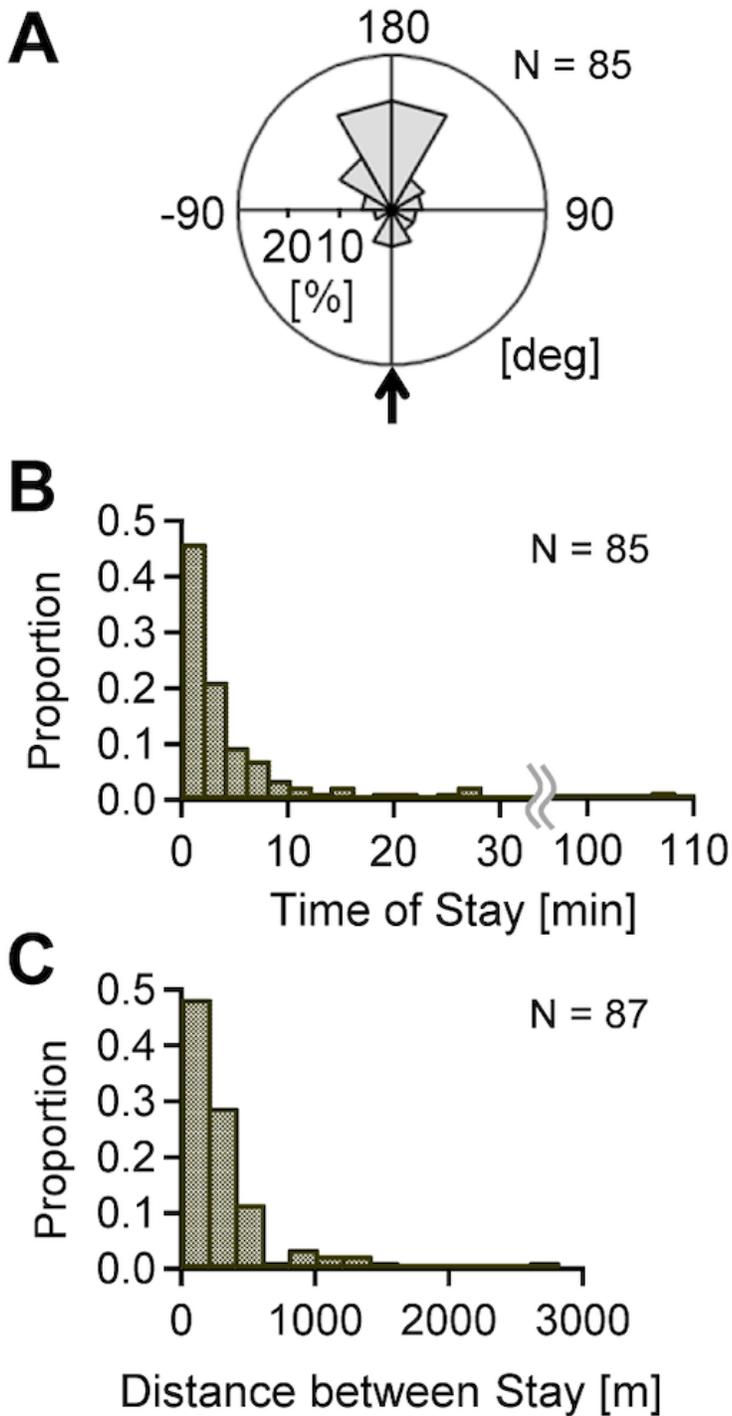


Figure 2

(A) Distribution of directions in which bats left the stay site relative to the direction of entry. Arrow indicates direction in which bats aimed to fly immediately before entering the stay site. (B) Proportional distribution of time bats spent at the stay site. If the start point of the trajectories of each bat was categorized as foraging-mode, the time of the first stay was not used (the same is true for the last stay).

(C) Proportional distribution of distances between two successive stay sites. A geodesic line was used to calculate distances.

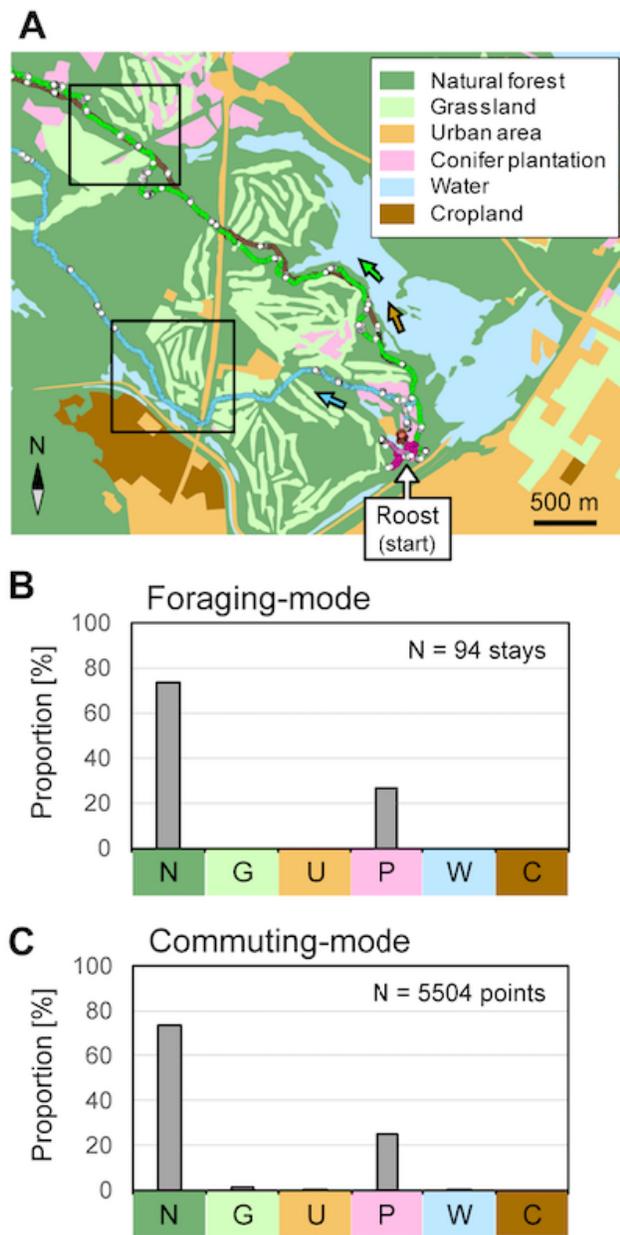


Figure 3

(A) Bat flight path shown on a land-use map of the area around the bat roost. Circles and arrows show paths and directions of bat flights, respectively. White circles indicate locations of foraging-mode

behavior. (B, C) Overview of proportions of GPS points associated with different habitat types during foraging (B) and commuting (C).

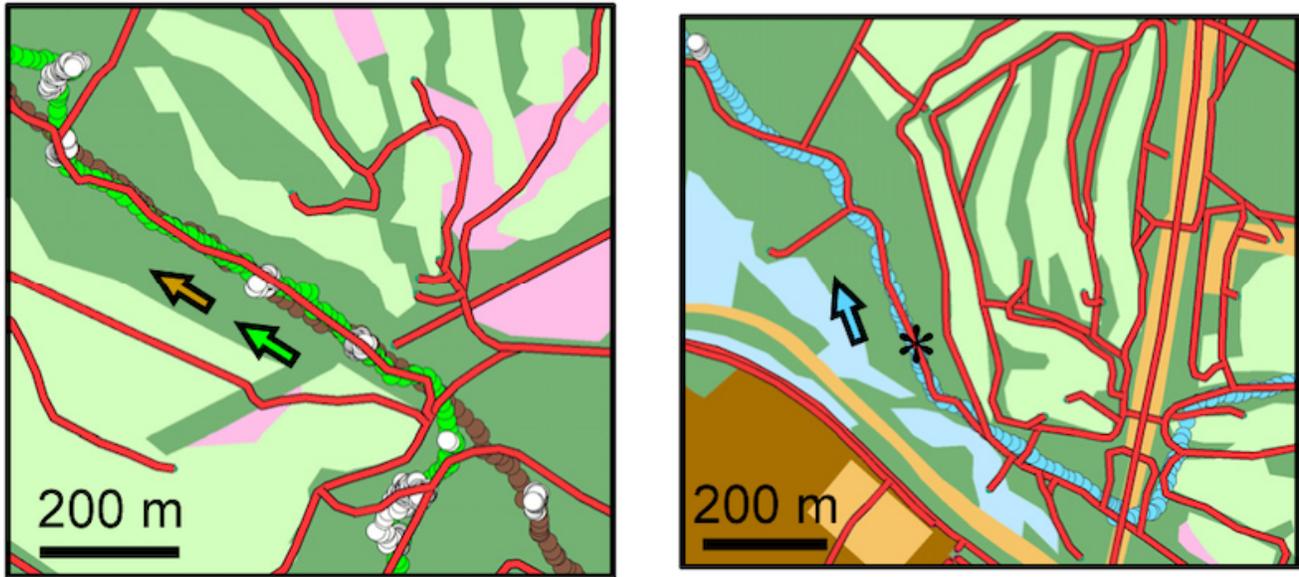


Figure 4

Magnified image of Figure 3A (squared portions). Red lines indicate roads traced from a map from the Geospatial Information Authority of Japan website. Asterisk in right figure indicates the position from which the photograph (Additional file 2) was taken.

Supplementary Files

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