Selection of 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).

Methods 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 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 preferences revealed that the bats preferred conifer plantation and natural forests as pathways and feeding habitats. Particularly, they locally traveled along forest roads at flight speeds significantly higher than those flown over other habitats.

Conclusions Our findings suggest the forests and their structures 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 air (< 10 m [4]), most studies have focused on small-scale relationships between bat echolocation and flight routes in 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. For example, the flight patterns of *Myotis* bats are associated with the predictability of prey occurrence [11]; 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 an local area while foraging. A state-switch between the two modes of commuting and foraging is the most basic behavior shown in animal movements [12]. However, there is still a lack of a unified understanding of continuous movements between the commuting and foraging of echolocating bats in the wild.

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 locate 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, horseshoe bats preferred a particular habitat type during foraging (pasture, forest, riparian vegetation, etc.). In addition, they flew 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, especially regarding the relationship between the flight paths and the habitats that they cross. To address this purpose, we used high-resolution GPS positions (i.e. logging every 2–3 s) for the greater horseshoe bat (*Rhinolophus ferrumequinum nippon*) during nightly foraging. We

hypothesized that the bats show the repetitive patterns of foraging and commuting, and both of the two modes in the bats' flight trajectory show a definite environmental preference during nightly movement. 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.

Methods

Bats and Study site

The target species of this study was *R. ferrumequinum nippon*, which has a body length and mass of approximately 6–8 cm and 20–30 g, respectively [22]. *R. ferrumequinum* 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 (Fig. 1A) 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*, but conifer plantations are patchy distributed. 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

Since this study is one of the very few bio-logging investigations of *R. ferrumequinum*, we attempted to obtain a holistic view of its nightly movement behavior by studying detailed flight paths in order to identify its feeding behavior as well as large-scale movement patterns over longer periods of time. We used two types of GPS data loggers in this study: PinPoint-50 (Biotrack, UK; 2.2 g; 0.3 g telemetry unit) and GiPSy-5 (Technosmart, Italy; 2.3 g). The PinPoint-50 units were set probatively 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 (Table 1). 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 zero if they failed to detect satellite signals for 300 s and 70 s, respectively. We shaved dorsal hair of each bat and attached one logger of either type using Skin Bond (Osto-bond, Montreal Ostomy Inc., Canada; Fig. 1A) 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. We caught and attached loggers to a total of 27 bats (GiPSy-5, 24; PinPoint-50, 3). 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 [23]. 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 [24, 25]. In this study, *R. ferrumequinum nippon* flight speeds were calculated to be similar to or greater than previously reported values [26, 27], 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.

Table 1
Summary of the bat flight data set 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 $\pm$ 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 $\pm$ 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 $\pm$ 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 $\pm$ 1.5 (N = 521)	Battery out
F	♀	GiPSy-5	3	2016/6/10	19:13	19:33	23:29	5298	72%	42	4.0 $\pm$ 1.7 (N = 1441)	Battery out
G	♀	GiPSy-5	3	2016/6/10	19:13	19:49	23:00	4101	80%	17	4.2 $\pm$ 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 transit-mode trajectory (see Fig. S2).												
*** GPS signal was temporarily lost during the period between 2:01–2:31.												

Data analysis

Since *R. ferrumequinum nippon* is considered to fly in forests [14], 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 1). 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 ($\max\text{-}d_{\text{window}}$) 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 $\max\text{-}d_{\text{window}}$ 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 $\max\text{-}d_{\text{window}}$ time series. In rare cases, e.g. when the logger was stationary, $\max\text{-}d_{\text{window}}$ 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. An example of the result of this procedure is provided in the Supplemental Information (Additional file 2). In previous studies, first-passage time analysis and state-space analysis have been proposed for the extraction of local search paths [12, 28]. 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).

Results

Overview

We collected data from a total of seven loggers (PinPoint-50, 2; GiPSy-5, 5; 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. 1B). 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 5 in details). We observed foraging trajectory patterns (Fig. 1C) among the flight paths of all bats. One of the seven bats remained at a single site for over 4 h (bat D); another flew away from a stay site and returned repeatedly to that site (bat C₂, Fig. 1D) in a foray search pattern [29, 30].

Properties of each mode

Since the bats were expected to forage at the stay site, we identified and focused on the foraging and commuting modes, analyzing these in detail; two bats tracked using PinPoint-50 loggers were excluded from this analysis because the trajectory was too rough (every 600 s logging). Figure 1E shows the amount of time spent in commuting throughout the entire measurement period. All bats, except Bat C₁, spent more than 70% of their time staying at different sites. Also, bats repeatedly switched between foraging and commuting modes. 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). Bat C₁ flew relatively long distances with 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 recorded in this study.

The bats usually left a stay point in the opposite direction from which they entered it (Fig. 1F), indicating that 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. 1G). 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. 1H).

Habitat preferences

We examined the habitat preferences of bats for commuting- and foraging-mode behavior (Fig. 2). The bats flew mainly toward natural forests (Fig. 2A). All stay sites visited by the five bats were either located in natural forests or in conifer plantations (Fig. 2B). Except of bat D that have only one stay site, the distribution of stay site habitat type of each bat's flight path was unbiased for three of the four bats (bats C, E, and G) ($p > 0.05$ except for bat F, χ^2 -test for goodness of fit). For also bat A and B that logged by PinPoint-50 (see Fig. 1), over 95% of measured positions belonged to the natural forest or conifer plantation. These results indicate that the bats flew mainly through natural forests and conifer plantations. To determine whether the bats intentionally flew over forests, we compared commuting time in each environment between bat flight trajectories of different commuting modes and a correlated random walk (CRW) [25, 31]. Thus, 100 CRW paths were produced for each bat (a total of 400 paths for all four bats); the flight speed, initial position, and turning angle at each step (degree of correlation) were equivalent to the bat's path (markers; Fig. 2C). This analysis showed that the proportion of commuting time spent in natural forest and conifer plantation environments (Fig. 2C) was significantly larger than that of a CRW (box plots; Fig. 2C). Similarly, the proportion of commuting time spent above urban areas, grassland, and water was lower than that of a CRW. These results indicate that forests were preferred for commuting and feeding habitat.

The forest road provided a sufficiently wide open space for a car to pass through (Additional file 3), and bats flew along this road (Fig. 2D). The average bat flight speed ranged from 3.8 to 5.3 m/s; three of the four bats had significantly higher flight speeds while flying along the road than while flying elsewhere (Fig. 2E, Welch's t-test). These results indicate that bats selectively traveled along the forest road during their nightly navigation; thus, anthropogenic structures can affect the flight paths of echolocating bats. The bats followed the road for approximately 30–50% of the total distance traveled in commuting mode (Fig. 2F). The GPS loggers used in this study recorded 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 [32, 33]. 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. ferrumequinum 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. ferrumequinum nippon* alternated foraging within a time frame of a few minutes. Also, bats commuted along forest roads during nightly movement, 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 [34–36]. Furthermore, habitat preference analysis revealed that the bats significantly preferred to commute and forage in a natural forest or conifer plantation rather than above grasslands or urban areas. In particular, the continuous information of the trajectory obtained with high-resolution GPS tracking allowed us to understand more clearly about the foraging behavior of this bat species. 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., roost for resting) by the Japanese greater horseshoe bat [14]. Since the sample size is small as a result of considering the effect on the individual, the results obtained in this study are of a descriptive nature. However, this is the first study to investigate nocturnal foraging of horseshoe bats in great detail using a GPS logger. We are confident that it will provide very valuable knowledge in order to advance the understanding of the ecology of this bat species in the wild.

Habitat preferences

We also verified the habitat selection of *R. ferrumequinum nippon* during nightly foraging activity with fine resolution after dividing the whole measured path into commuting and the foraging modes. Several factors may cause these habitat preferences for the bats in our study site. First, forests are suitable for the flycatcher feeding style due to the abundance of tree branches. Second, *Rhinolophus* species generally have large wingtips and low aspect ratio, for slow flying and good maneuverability [37]; flying within forests allows bats to avoid predators and harsh weather. Third, forests are a major source of flying insects, which are consumed by *R. ferrumequinum*. In a previous study conducted in the UK using radio telemetry, this bat species preferred to fly over pastures and in forests [19, 38], 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. Such a difference in the environmental preference might be caused by the availability of prey items in each environment. In the future, it will be necessary to investigate the habitat use of this bat species according to each environment.

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 [39–41]. Our high-resolution GPS bio-logging study demonstrated that bats commuted locally along a forest road at higher flight speeds than in other habitats (Fig. 2). Such a route-following behavior is one of the various large-scale navigation strategies of bats that have been previously reported [42], 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.

Properties of each mode

Our results showed that the mode of the stay period distribution was 0–2 min, and for one individual up to 10 stays per hour were confirmed. In all cases, bats chose to stay at a series of sites one after another on their way from the roost to another location (Fig. 1F). These stay sites did not overlap among individuals during the measurement period. Therefore, bats likely do not aim towards a specific foraging site, but repeatedly stay at various stay sites such that each bat can forage.

We recorded two cases of unrepeated commuting and foraging in (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 (C_2 ; Fig. 2E). 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 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 [43–45] for mating [46, 47] 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 have traveled a long distance because of unknown social behavior in mating season. In contrast, bat D stayed continuously at a single site near the roost for over 4 h early in the night (Fig. 1D, E) (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 4), 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 1). 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, 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 [24, 25]. 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 [48] and bats [23]. A previous study showed that no significant differences were observed between the behavior of echolocating bats (*M. myotis* and *M. vivesi*) carrying loggers with 15% of their body weight and non-tagged individuals [11]. 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 [26, 27], suggesting that the influence of the data logger weight on bat flight performance was negligible. Nevertheless, 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 no 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 succeeded in recovering the data from 7 individuals only. 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 preferred to commute and forage in natural forest or conifer plantation, and commuted locally and reliably along a forest road. 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.

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 5.

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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Figures

Figure 1

GPS tracking of echolocating bats during nightly flight navigation. (A) GPS data logger wrapped in thin gauze and attached to the back of the bat. (B–D) Measured flight trajectories of bats drawn on large- (B), medium- (C), and small-scale (D) satellite images. Arrows represent bat flight directions. (E) Activity of each bat measured during a logging night. Gray shading indicates the period when loggers could not capture the satellite signal. Colored shading indicates foraging and commuting modes when the vertical values were 0 and 1, respectively. Orange vertical lines indicate sunset. (F) Distribution of directions in which bats left the stay site relative to the direction of entry. Arrows indicate directions in which bats aimed to fly immediately before entering the stay site. (G) Proportional distribution of time bats spent at the stay site. (H) Proportional distribution of distances between two successive stay sites. A geodesic line was used to calculate distances.

Figure 2

Bat flight properties in commuting and foraging mode trajectories. (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. Dark green, natural forest; light green, grassland; orange, urban area; pink, conifer plantation; blue, water; brown, cropland. (B) Proportion of area covered by stay sites for each bat. Numbers on the upper side of each bar indicate the number of stays. (C) Proportion of area over which bats flew in commuting mode (circle). Box plots represent correlated random walk behavior based on the flight pattern of each bat. (D) Magnified image of (A). Red lines indicate roads traced from a map from the Geospatial Information Authority of Japan website. Asterisk in (D-b) indicates the position from which the photograph (Additional file 3) was taken. (E) Flight speed (mean $\pm$ standard deviation, SD) of each bat flying along the forest road (filled circles) and elsewhere (open circles) were 5.30 ± 1.95 m/s and 5.00 ± 1.85 m/s (bat C, $n = 1717$ and 929 , $p < 0.01$), 3.83 ± 1.59 m/s and 3.76 ± 1.48 m/s (bat E, $n = 279$ and 242 , $p = 0.65$), 4.23 ± 1.99 m/s and 3.94 ± 1.54 m/s (bat F, $n = 1021$ and 420 , $p < 0.01$), and 4.72 ± 2.93 m/s and 3.83 ± 1.70 m/s (bat G, $n = 480$ and 323 , $p < 0.01$). Bats were defined as flying along the road if located within a distance of 30 m from the road. (F) Percentage of distances flown along the road as a function of total commuted distance.

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