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High-Resolution GPS Tracking of Perch-Hunting Bats, *Rhinolophus nippon*, During Nightly Foraging Behavior

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While the echolocation behavior and specialized adaptive auditory system of the greater horseshoe bat *(Rhinolophus ferrumequinum)* are well documented, comprehensive insights into its wild ecology, especially its detailed nocturnal movements for foraging behavior, remain scarce. Therefore, our objective was to obtain information on the spatiotemporal features of the movements of the Japanese greater horseshoe bat (*Rhinolophus nippon*), a close relative of *R. ferrumequinum*, during foraging. Hence, we investigated the nightly flight paths of *R. nippon* using high-resolution GPS data loggers. Initially, hidden Markov modeling analysis classified bat flight paths into two behavioral patterns: commuting and area-restricted behavior, the latter primarily corresponding to foraging activities. Focusing on foraging behavior along their trajectory, we observed that *R. nippon* repeatedly foraged with brief stops lasting only a few minutes and an average distance of approximately 300 m between any two foraging sites. Notably, one individual covered a considerable distance (23.6 km) from its roost, possibly because of irregular social behavior during the mating season. Furthermore, for commuting, bats occasionally used forest roads, which were located along the middle of relatively steep slopes. In cases of echolocations with limited detection distances, echoes from the ground and adjacent tree lines offered crucial navigation cues, underscoring the significance of forest roads as nightly movement routes for echolocating bats. Overall, our findings highlight the importance and urgency of ongoing research on bat movement ecology in Japan.

Key words: bio-logging, movement, navigation, horseshoe bat, hidden Markov model, step selection function

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INTRODUCTION

Animals choose routes toward their destinations based on their innate sensing systems and behavioral strategies (Bartumeus et al., 2005; Nathan et al., 2008). In particular, except for species in the family Pteropodidae, most bat species produce laryngeal echolocation sounds to obtain information about their immediate surroundings when light and other cues are unavailable (Griffin, 1958). Owing to the limited range of echolocation calls using ultrasound, which typically do not propagate over long distances through the air, the detection range using echoes is quite short, typically less than 10 m (Schnitzler et al., 2003). Consequently, many studies on echolocating bats have traditionally focused on small-scale movements in laboratory settings or small field experiments (Ghose et al., 2006; Chiu et al., 2008; Kounitsky et al., 2015; Fujioka et al., 2016; Sumiya et al., 2017). Recently, technological advances in the design of animal-borne devices have opened new avenues for research on bat movement on a much larger spatial scale; concomitantly, bio-logging (i.e., storing data within tags) has accelerated the investigation of the movement ecology of echolocating bats in the wild (Rutz and Hays, 2009). Thus, for example, a GPS-tracking study revealed that the flight patterns of *Myotis* bats are associated with the predictability of prey occurrence (Egert-Berg et al., 2018); specifically, the mouse-eared gleaning bat, *M. 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

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the ocean in search of ephemeral resources and exhibits intensive movement patterns in a local area while foraging.

The Japanese greater horseshoe bat (*Rhinolophus nippon*) is a large *Rhinolophus* species that is widely distributed in East Asia. Until recently, it was treated as the same species or subspecies as *R. ferrumequinum*, which is widely distributed from Europe to Central Asia, but in recent years, it has been treated as a separate species as a result of molecular phylogenetic analysis (Ikeda and Motokawa, 2021). *Rhinolophus nippon* is known to forage for large insects, such as moths, mainly in a perch-hunting style, which is characterized by hanging from a tree branch while searching for prey, and flying off for capture (Funakoshi and Maeda, 2003) using high duty cycle echolocation (Matsuta et al., 2013). To understand the foraging and commuting habitat use of horseshoe bat species, it is necessary to track their nocturnal foraging trajectories in detail and to measure the foraging sites selected by individuals, along with their movement trajectories. In Europe, through examination of their ranging and foraging patterns, previous studies using radio-tracking (Stebbings, 1982; Duvergé and Jones, 1994; Bontadina, 2002; Billington, 2003; Flanders and Jones, 2009; Dietz et al., 2013)—and more recently, GPS-tracking (Jeon et al., 2018)—have shown that closely related species *R. ferrumequinum* prefers certain habitat types (e.g., pasture, forest, and riparian vegetation). However, no study has revealed the movement trajectory of *R. nippon* to date. Moreover, to the best of our knowledge, there are no reports on detailed tracking of the nocturnal foraging trajectories of either *R. nippon* or *R. ferrumequinum* using, for example, GPS-tracking with a resolution high enough to allow the identification of foraging sites, whose importance is beginning to be recognized (Nathan et al., 2022).

In this study, we conducted a bio-logging survey of flight trajectories of *R. nippon* using loggers with short tracking durations but high resolution and loggers capable of overnight tracking, to investigate the basic nightly movement patterns and habitat use of these bats. Based on the perch-hunting foraging style of the species, the flight trajectories of the bats were expected to reveal area-restricted movement through foraging behavior and commuting flight (Roeleke et al., 2022). Hence, we extracted these types of behavior from the GPS-based localization of bats to analyze their behavioral patterns and habitat use.

MATERIALS AND METHODS

GPS logging

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). The target species of this study was *R. nippon*, which has a body length and mass of approximately 6–8 cm and 20–30 g, respectively (Matsuta et al., 2013). Generally, this species uses underground sites, such as caves and abandoned tunnels, as well as abandoned buildings, as day and night roosts (Sano, 2015). Females form tightly packed maternity colonies with 10–200 individuals in summer (Sano, 2015). *Rhinolophus nippon* begins to forage shortly after sunset and hunts flying insects mainly in a perch-hunting style (Funakoshi and Maeda, 2003). Bats were captured with butterfly nets at their day roost, an abandoned pillbox in Tomakomai, southern Hokkaido, Japan (42°41′00.2″N 141°40′13.1″E), during daytime on a total of 7 days: 2 June and 3 September 2015; 10, 11, and 12 June 2016; and 2 and 5 September 2016. All bats were tagged with numbered aluminum rings (4.2 mm, Lambournes Ltd., Leominster, England) attached to their forearms. A forest and golf course are located north of the roost, and an urban area lies to the south. The forest is mainly a natural secondary forest dominated by *Quercus crispula* with interspersed patches of conifer (*Larix kaempferi*) plantations.

Two different types of loggers were used. The first was a high-resolution GPS logger (GiPSy-5, Technosmart, Italy, 2.3 g) that can record fine movements with high resolution (log every 2 or 3 s continuously for approximately 4 h). The second was an overnight logger (PinPoint-50 data logger, Biotrack, UK, 2.2 g, including 0.3 g wireless transmitter unit) that can capture a holistic view of the nightly movement behavior (every 600 seconds for approximately 9 hours). We attached either of these two types of loggers to 27 bats (24 GiPSy-5s, two males and 22 females; three PinPoint-50s, all females) and collected data from seven loggers (GiPSy-5, five; PinPoint-50, two; Table 1) (see DISCUSSION for details). In accordance with the previous report that approximately 90% of *R. nippon* individuals became active approximately 4 h after sunset (Funakoshi and Maeda, 2003), we set a timer to start data logging at 19:00 (around sunset time, see Table 1). To exclude any effect of logger attachment on bats, the positions of actively foraging bats were measured on the second day after attachment. Data loggers continued to measure the active flight paths until the batteries were depleted (Note that the GiPSy-5 and PinPoint-50 units were set to

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

Bat	Sex	Body Weight [g]	Logger Type	Log Interval [s]	Measure Date	Sunset Time***	Log start Time	Log end Time	No. Points	Ratio ARB [%]	No. ARB Sites
A	♀	29	PinPoint	600	Jun. 2–3, 2015	19:08	20:15	27:00	38	—	—
B	♀	26	PinPoint	600	Jun. 2–3, 2015	19:08	20:05	25:30	27	—	—
C_1	♂	≥ 23	GiPSy	2	Sep. 4, 2015	18:07	25:30	27:50**	3536	29.9	21
C_2	♂	≥ 23	GiPSy	2	Sep. 5, 2015	18:06	24:16	24:34	544	66.4	11
D	♀	≥ 23	GiPSy	2	Sep. 3, 2015	18:07	19:30	23:45	8002	100*	—
E	♀	24	GiPSy	3	Jun. 10, 2016	19:13	19:32	23:42	5156	89.8	35
F	♀	25	GiPSy	3	Jun. 10, 2016	19:13	19:32	23:29	5298	70.8	76
G	♀	23	GiPSy	3	Jun. 10, 2016	19:13	19:49	23:00	4101	82.0	28

Bat C was divided into C1 and C2 because the logger recorded data for 2 consecutive days.
The body weight data when logger attachment in Sep 2015 was lost but it was confirmed to be at least 10 times the weight of the logger.
* All points were defined in the ARB mode because there was no clear commuting pattern.
** GPS signal was temporarily lost during the data collecting period from 26:01 to 26:31.
*** Data from National Astronomical Observatory of Japan were used.

sleep for 15 min and output a zero value if they failed to detect satellite signals for 300 s and 70 s, respectively). The weather data (weather, wind speed, and direction) during the logging period was sourced from the Japan Meteorological Agency (www.jma.go.jp). Wind speed and direction were defined as the average values and direction during the logging periods for each tagged bat.

The loggers were attached using a Skin Bond (Osto-bond, Montreal Ostomy Inc., Canada) after removing a small area of dorsal hair from each bat outside the roost. Bats were held for approximately 10 min in addition to the time of logger attachment and measurement (body mass, forearm length) to allow the glue to dry prior to their release into the roost. Body mass was measured by using an electronic scale (Handy-mini-1476; TANITA, Tokyo, Japan). GiPSy-5 and PinPoint-50 units weighed 2.3 g and 2.2 g, respectively; i.e., in both cases, less than 10% of the weight of the bats measured (> 23 g) in this study. The logger-to-body weight ratio was greater than 5% of the body mass threshold recommended for bats (Aldridge and Brigham, 1988). 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 in foraging behavior or body mass (Cvikel et al., 2015; Roeleke et al., 2016). In this study, there were no distinct changes in body weight between initial capture and recapture (–1 g for all three bats in 2016, no data in 2015). Furthermore, when individuals that had been tagged in the previous year were coincidentally recaptured the following year or later, the back fur of the bats had completely regrown, suggesting that there was virtually no effect of tagging on the individuals that could be observed.

The attached loggers were collected by recapturing on the day after attachment to the roost. A remover (Uni-Solve Adhesive Remover; Smith and Nephew, UK) was used to remove the loggers as gently as possible from the backs of the bats. The datasets generated and analyzed during the current study are available in the Movebank Data Repository (Fujioka et al., 2024).

When *R. nippon* bats fly under a forest canopy, the GPS measurement error may be relatively high. Therefore, we measured the positional errors of the data loggers at three sites in the forest near the roost. High-resolution GPS loggers (GiPSy-5) were installed at the site and the degree of change in coordinates was examined while the loggers were stationary. Measured positional errors 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 directions (see Supplementary Figure S1).

Data analysis

Clustering

In previous studies, several clustering methods have been assessed for the extraction of local searches for foraging events using trajectory data, and the hidden Markov model (HMM) performed best at identifying fish-eating bat foraging segments (Hurme et al., 2019). Therefore, in this study, we used the HMM to cluster bat movement states. The HMM clustering should extract the trajectory pattern of foraging with area-restricted search (ARS) behavior because *R. nippon* searches and captures insect prey by perch-hunting (Schnitzler et al., 1985). Such a trajectory pattern is termed "area restricted movement" (ARM) (Roeleke et al., 2022). However, since it cannot rule out the possibility that the bats take a rest while hanging on the tree (i.e., roosting [RST] mode), it should be difficult to distinguish between RST and ARM. Thus, in this study, 2-state HMM was conducted using the fitHMM function in the R package 'momentuHMM' version 1.5.5 to divide bat trajectories into commuting (COM) mode and area-restricted behavior (ARB) mode, which contained both ARM and RST during perching.

The step length and turning angles used as parameters for the HMM were defined as the distance between two successive logged positions from the current (p_n) to the next (p_{n+1}) positions and the difference in flight direction between two successive steps from the current (p_{n-1} -> p_n) to the next (p_n -> p_{n+1}) steps, respectively. Step length was recalculated as distance per second (i.e., flight speed). The distributions of the step length and the turning angles were adopted from gamma and von Mises distributions, respectively; in turn, the initial value of step length was determined by fitting, for which purpose, the mixed normal distribution of the step length of all individuals was obtained by applying the normalmixEM function in the R package 'mixtools' version 2.0.0 (Hurme et al., 2019).

To evaluate the result of the 2-state HMM, we used the position data of the installed stationary loggers, which was assumed to be virtual RST data (see Supplementary Text 1). Values for the step length and turning angle of the installed stationary logger data were estimated using the gamfit function in Matlab and the mle.vonmises function in the R package 'circular' version 0.4-95, respectively. Then, we compared the estimated parameters between the installed stationary logger and the moving bats. Bats tracked by PinPoint-50 loggers were excluded from this analysis, because their trajectory was too coarse compared to the duration of ARB-mode observed by GiPSy-5s.

Habitat analysis

Geographical information system (GIS) analysis was performed using ArcGIS Desktop 10.4 software (Esri Japan Corporation). The land-use map data used in this study was downloaded from the Ministry of Land, Infrastructure, Transport, and Tourism website (nlftp.mlit.go.jp). Habitats were categorized into the following six groups: natural forests, grasslands, urban areas, conifer plantations, water areas, and croplands. There are many edge spaces not only at the boundaries of these habitats but also within the latter. As there is no data with regard to such edge spaces, we examined the area in which the coordinates of the bats were located regardless of their proximity to the edge space. To also examine whether the bats fly along the road, positional data of roads was traced from a map from the website of the Geospatial Information Authority of Japan.

To investigate habitat selection of animals, the resource selection function (RSF) and step selection function (SSF) have recently been used as powerful tools (Fieberg et al., 2021). In particular, modeling SSF and estimating its selection score using logistic regression with GPS trajectory data is beneficial for analyzing continuous tracking data (Thurfjell et al., 2014). In this study, we used SSF to investigate habitat selection by the bats. To account for individual differences, the SSF modeling was performed based on Muff et al. (2020), using the glmmTMB function from the R package 'glmmTMB' version 4.2.3. Only COM-mode trajectory data after the HMM analysis was utilized in this study, as ARB-mode data is expected to contain substantial periods when the bats did not move.

We used three covariate datasets: (1) land use, (2) elevation, and (3) distance to road. (1) The land-use map data was downloaded from nlftp.mlit.go.jp (see above). (2) We obtained 5-meter mesh elevation data from the Basic Geospatial Information provided by the Geospatial Information Authority of Japan (https://fgd.gsi.go.jp/download/menu.php). Elevation is referenced to the mean sea level of Tokyo Bay. (3) Road positional data was traced from a map provided by the Geospatial Information Authority of Japan. For all three datasets, raster data was created using the 'Near' tool in ArcGIS Pro version 3.0.3 (Esri Japan Corporation), and GeoTIFF files were generated using the geotiffwrite function in the MATLAB Mapping Toolbox. The continuous variables, elevation and distance to roads, were normalized using the scale function in R to enhance interpretability.

To create random steps for SSF, we used a slightly modified version of the random_step function from the R package 'amt' version 4.2.3. This custom function was designed to ensure the output is of vector type. The track_resample function from the amt package generates a valid step sequence (burst) when COM mode points are present at specified sampling steps, even if the burst contains ARB mode points clustered by the HMM. To achieve this, we resampled GPS data and created bursts using MATLAB. The resampling interval was set to one minute due to the small sample size. The Wald test was employed to assess the significance of selectivity for each categorical variable.

RESULTS

Overview

Figure 1A shows the nightly movements of the two bats recorded by an overnight logger. The success rates of GPS positioning for bats A and B were 55% and 47%, respectively. The bats left the roost (i.e., logging started) within approximately 1 h after sunset, similar to the previously reported times of emergence for *R. nippon* obtained by visual observation (Table 1) (Funakoshi and Maeda, 2003). Bat A started moving at 20:15, and its travel track turned at a point 14 km away from the roost, and its final position was recorded at 3:00 at a distance of 2.6 km from the roost. Bat B departed the roost at 20:05, and its final position, at 1:30, was approximately 8.5 km from the roost, and then it did not log positions for over an hour until sunrise. These two bats returned to different roosts from those to which they returned the previous day.

Based on the records of the overnight logger, the recording period of the five bats equipped with the high-resolution logger corresponded to the period of foraging activity, when the bats were flying away from their roosts (Fig. 1B). Figure 2 shows the GPS trajectory data of these five bats; in general, they flew in a northwest direction from the roost (Fig. 2A), the same as the bats with the overnight logger attached to them, while

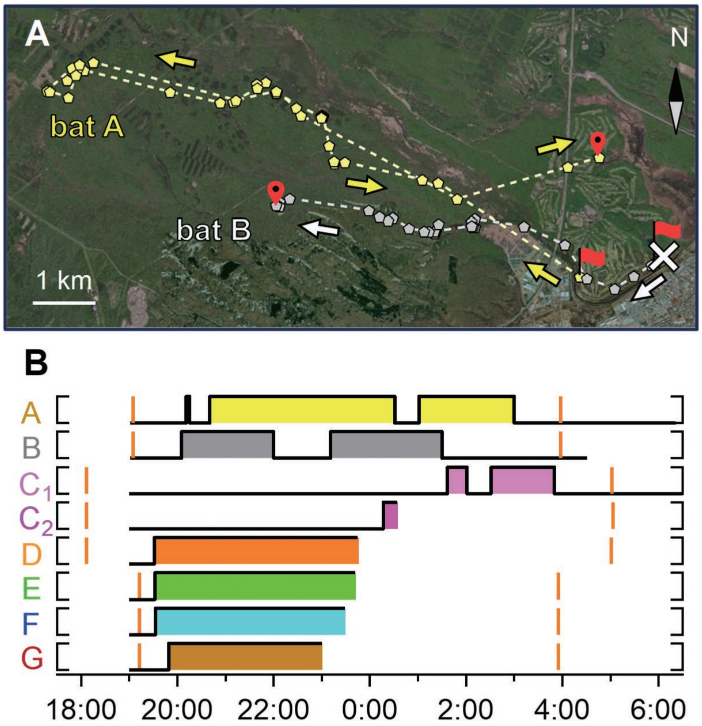

Fig. 1. Overview of the logging record of the nightly foraging activity. **(A)** Whole flight trajectories of the bats during nightly foraging; drawn on the satellite image. Red flags and pins show the start and last logged positions, respectively. Arrows represent bat flight directions. The cross mark indicates the roost. **(B)** Time series of logging record of all collected loggers. The logged time period was colored. The end of each black line indicates the time the battery was exhausted. Orange vertical lines indicate the timing of sunset (left) and sunrise (right).

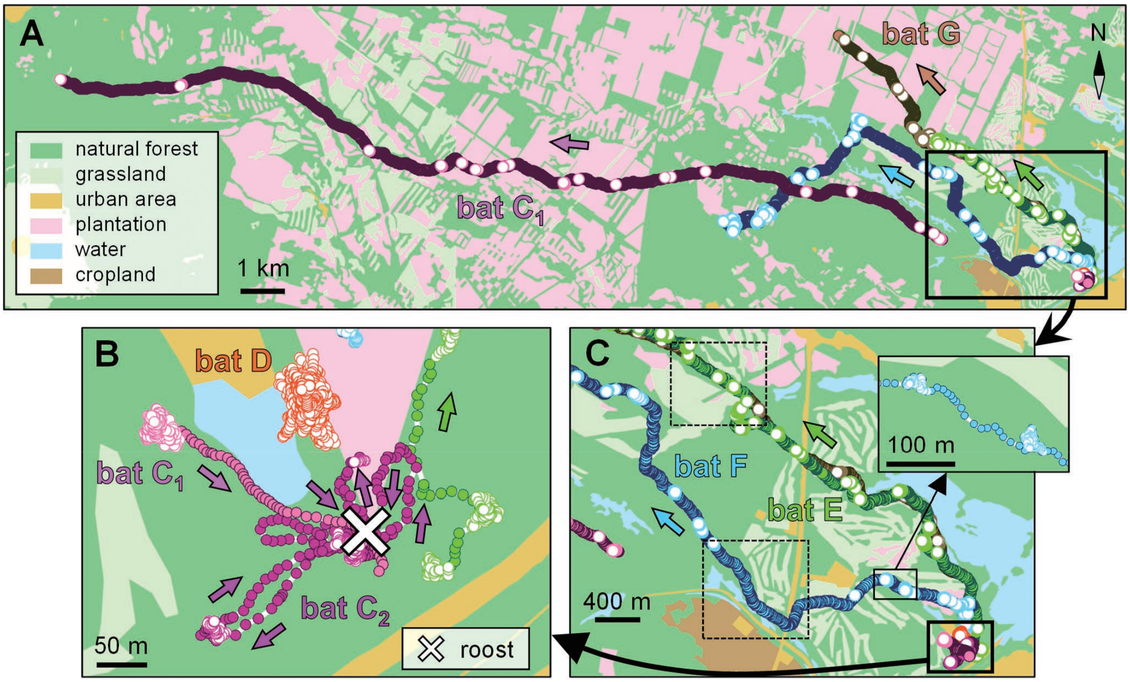

Fig. 2. Bat flight trajectories measured by high-resolution GPS tracking at large- **(A)**, small- **(B)**, and medium-scale **(C)** land-use map provided by the Ministry of Land, Infrastructure, Transport and Tourism. Arrows represent bat flight directions. White circles indicate locations of ARB-mode behavior identified by HMM analysis. GPS signal for bat C_1 was temporarily lost for 30 min (see Table 1 for details). Flight paths enclosed within dotted squares are shown in Fig. 5.

one bat remained at a single location for over 4 h (bat D in Fig. 2B). Bat C_1, shown in Fig. 2A, flew almost directly northwest for a distance of 23.6 km, which was the longest flight distance recorded in this study. Note that there was data for 2 days for bat C (C_1 and C_2), because the battery did not run out overnight. No individual returned to the roost where the GPS loggers had been attached immediately after the end of data logging. Lastly, although bat D was caught in drizzling rain for approximately 1 h around 23:00, the weather was clear or cloudy during all measurement periods for the other bats (bat A, B, C, E, F, and G). The wind blew from a generally northern direction (between northwest and northeast) during the logging periods for all bats except bat D. The wind conditions were as follows: bat A: 1–2 m/s from the northeast (outward trip), 1 m/s from the northwest (return trip); bat B: 1–2 m/s from the northeast (outward trip), 1 m/s from the north (return trip); bat C_1: 2 m/s from the northwest; bat C_2: 1 m/s from the north; bat D: 1–4 m/s from the west; bats E, F, G: 3–4 m/s from the north.

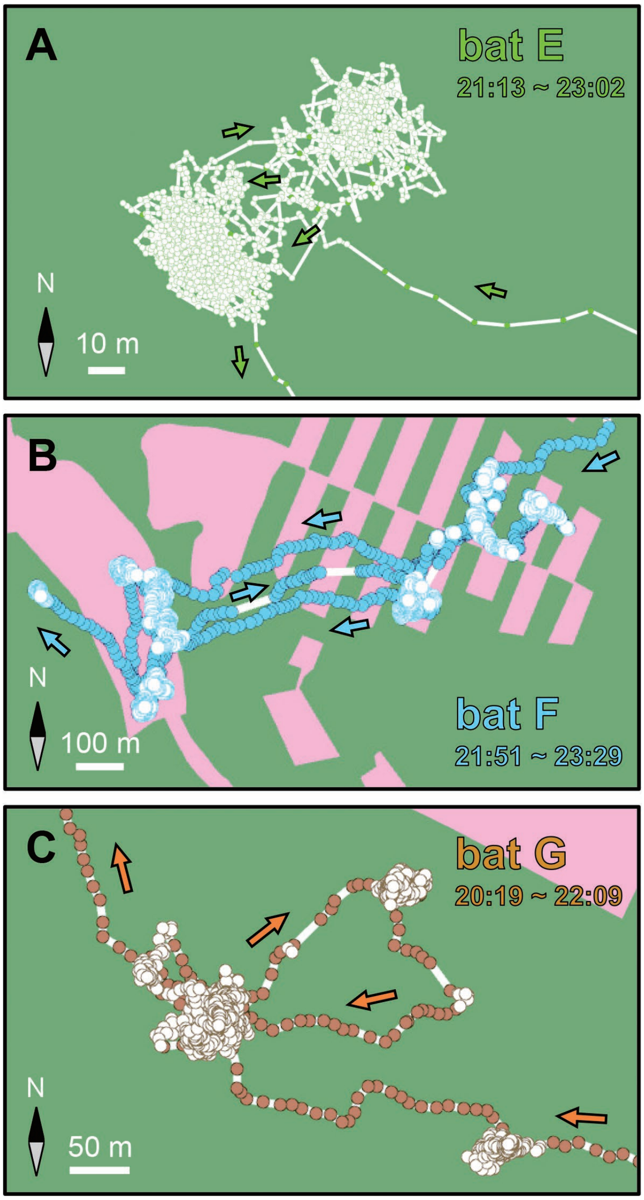

Fig. 3. Part of the flight path of bats E **(A)**, F **(B)**, and G **(C)**, while returning to a location where the bat was previously detected in ARB mode. The arrows indicate the direction of bat movement.

Movement pattern

Analysis through HMM (see Supplementary Figure S2) revealed that the bats repeated the ARB pattern during nightly movement (white circles in Fig. 2). Except for bat C_1, which showed the longest flight in this study, all bat flights tracked with a high-resolution logger showed a longer duration in ARB than in COM mode (Table 1). We recorded a

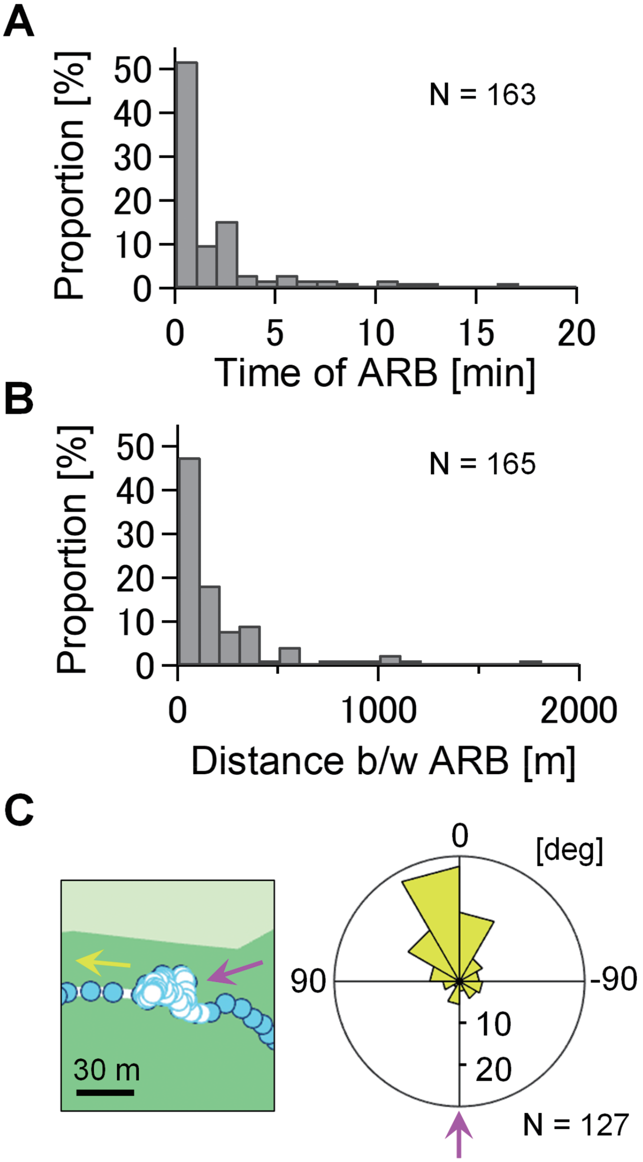

Fig. 4. Characteristics of the ARB-mode flight pattern recorded for the bats under study. **(A, B)** Proportional distributions of time bats spent at ARB **(A)**, and distances between two successive ARB sites **(B)**. The representative location of an ARB was calculated as means of longitude and latitude each in the ARB. A geodesic line was used to calculate distances. **(C)** Distribution of directions in which bats left ARB (yellow) relative to the direction they entered ARB sites (magenta).

maximum of 76 ARB sites (clusters of GPS data points classified as ARB) for Bat F for a 237-min recorded trajectory; furthermore, the ARB site of each bat did not overlap between the recorded flight trajectories in this study. A closer look at the vicinity where ARB sites were observed revealed repeated visits to the same site for all bats monitored in this study, except for bat D (Fig. 3, bat C_2 in Fig. 2B).

The time that bats displayed an ARB pattern was 185 ± 335 s (mean ± SD, n = 163), and more than half of the recorded ARB flights lasted only less than 1 min (Fig. 4A). The distance between consecutive ARB sites was 304 ± 538 m (mean ± SD, n = 165), and approximately half of such distances were less than 100 m (Fig. 4B). Bats exited ARB sites in a direction opposite to that in which they entered (the exiting direction relative to that of entering the ARB site was concentrated around 0 deg; mean ± SD: 10.4 ± 70.3 [deg], n = 127, Fig. 4C), indicating that they repeatedly performed ARB along the nightly movement route.

Habitat use

Almost all of the habitats were either natural forests (88.3%) or conifer plantations (11.5%) (Table 2) during the ARB flight mode (white circles in Fig. 2). Similarly, almost all habitats in the COM flight mode were forested areas (73.5% and 25.0% for natural forest and conifer plantations respectively; Table 3). Similarly, for bats A and B when logged by overnight loggers, over 95% of the measured positions corresponded to natural forests or conifer plantations.

In the forests, bats were often observed flying along the roads (Fig. 5). Here, we calculated the shortest distance from all logged positions to the roads and defined those less than 25 m (error = 3σ) as the data at which bats flew along the roads. As a result, 33.4% and 42.7% of the measured positions in COM and ARB flight modes were identified as along-road data, respectively (Tables 2, 3). Such route-following behavior was observed in the forest for all cases and the bats tended to fly at right angles to the slope direction on relatively steep slopes (Fig. 5B).

The results of SSF modeling using only COM-mode data show that the preference for forests (natural forests and conifer plantations) was significantly higher than that for other environments (grassland, urban areas, cropland, and water) ($P < 0.05$, Wald test; Fig. 6 and see Supplementary Table S1). Regarding land elevation, the 95% confidence interval (CI) for the regression coefficient was distributed less than 0, indicating a significant tendency to fly at lower altitudes ($P < 0.01$, Wald test, Fig. 6 and see Supplementary Table S1). For distance to the road, the 95% CI for the regression coefficient was around 1, with no significant tendency observed for proximity to or distance from roads (P = 0.25, Wald test, Fig. 6 and see Supplementary Table S1).

The high-resolution loggers used in this study can also record altitude data, but their accuracy is low, as indicated by the fact that stationary loggers placed 1 m above the ground in the forest recorded the height as 8.3 ± 12.3 m (mean ± SD; 95% confidence intervals [CI], 7.6–9.1; n = 985). Furthermore, the height that the the same type of loggers recorded when worn by individuals walking on the forest road near the roost was 15.0 ± 12.7 m (mean ± SD; 95% CI, 14.1–15.9; n = 784), which was slightly higher than when they were station-

Table 2. Attributes of ARB mode GPS points; proportions of each land use type (left) and of fixes near the road (right).

Bat ID (No. points)	Natural Forest	Grassland	Urban area	Conifer plantation	Water	Cropland	R_{road} < 25 m**
C_1 (926)	81	0	0	19	0	0	80
C_2 (344)	97.7	0	0	2.3	0	0	98
D (7613)	96.5	0	0	3	0.5	0	99.7
E (4487)	100	0	0	0	0	0	35.3
F (3342)	48	0	0	52	0	0	28.2
G (3128)	95.7	0.1	0	4.2	0	0	49.3
Total* (19840)	88.3	0	0	11.5	0.2	0	42.7***

* Percentage of each land use in all ARB-mode GPS points.
** Ratio of points within 25 m of roads.
*** Values estimated by multiplying the ratio of points ranged within 25 m from the roads by the number of ARB sites (see Table 1) rather than the number of points belonging to an ARB to avoid bias due to differences in measurement points for each bat.

Table 3. Attributes of COM flight mode GPS points; proportions of each land use type (left) and of fixes near the road (right).

Bat ID (No. points)	Natural Forest	Grassland	Urban area	Conifer plantation	Water	Cropland	R_{road} < 25 m**
C_1 (2162)	68	0.9	0	31.1	0	0	27.2
C_2 (174)	93.7	0	0	6.3	0	0	86.8
D	–	–	–	–	–	–	–
E (507)	96.8	1.2	0.4	1.6	0	0	37.3
F (1377)	68.6	1.7	0.1	29.3	0.4	0	30.3
G (688)	78.6	1.7	0.1	19.5	0	0	42.7
Total* (4908)	73.5	1.2	0.1	25.0	0.1	0	33.4

* Percentage of each land use in all COM flight mode GPS points.
** Ratio of points within 25 m of roads.

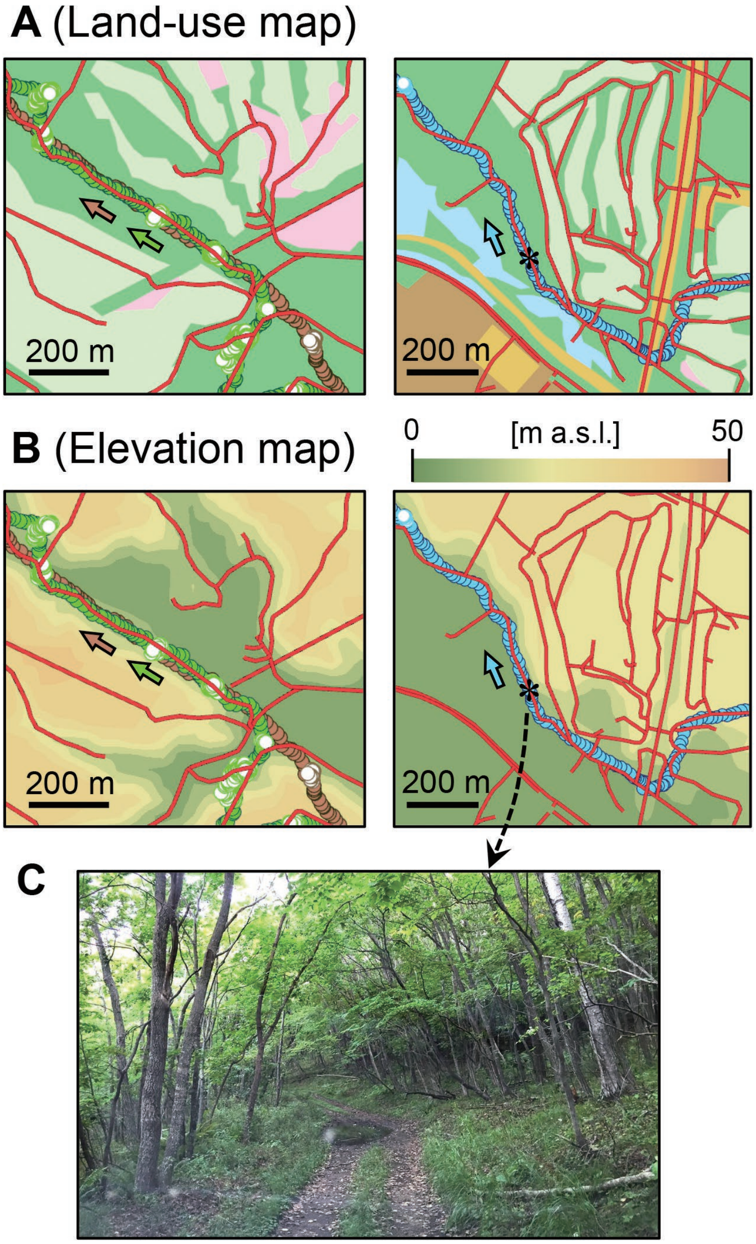

Fig. 5. Trajectory patterns of the bats flying along the road. **(A, B)** Magnified flight paths enclosed by dotted squares in Fig. 2C on **(A)** the land-use map and **(B)** the elevation map. Red lines indicate roads traced from a map from the website of the Geospatial Information Authority of Japan. The asterisk in the panels on the right indicates the position from which the photograph **(C)** was taken.

ary. These results are expected to bias the error toward the positive side. The height of bats above the ground recorded while in COM flight mode was 16.7 ± 18.1 m (mean ± SD; 95% CI, 16.2–17.2; n = 4908), and given the positive bias of the altitude data, the bat height during COM mode was clearly lower than the canopy height of the study area (approximately 15–20 m [Ishii et al., 2004; Hayashi et al., 2013]).

DISCUSSION

Movement pattern of *Rhinolophus* bats

Greater horseshoe bats, a species closely related to *R. nippon*, are a particularly well-studied high duty cycle species in terms of their echolocation behavior and specially adapted auditory systems (Schnitzler and Denzinger, 2011; Fenton et al., 2012). However, reports on their ecology in the wild, particularly on their detailed nocturnal movement and foraging are scarce at best (Schnitzler et al., 1985; Flanders and Jones, 2009; Jeon et al., 2018). In this study, for the first time, we tracked the nocturnal movements of *R. nippon* using high-resolution GPS loggers, and succeeded in obtaining information on the spatiotemporal features of repeated ARB sites with regard to their movements during foraging behavior. Based on the characteristic perch-hunting foraging style of this species (Schnitzler et al., 1985), bats fly back to the positions where they perch before attacking their prey; further, the ARB and COM modes into which flight patterns were categorized in this study supposedly correspond to foraging and commuting, respectively (Note that, strictly speaking, the ARB mode might also include roosting, RST. However, it is inferred to be ARM for foraging due to their foraging style (Schnitzler et al., 1985) and their active time zone for nightly foraging (Funakoshi and Maeda, 2003)). If an ARB is assumed to reflect a foraging site (Hurme et al., 2019), *R. nippon* individuals repeatedly foraged on their nightly movement routes, but each stay was short, lasting only a few minutes, and the average distance between foraging (i.e., ARB) sites was approximately 300 m (Fig. 4). Since the greater horseshoe bat can also forage in an aerial-hawking style (Jones and Rayner, 1989), they might forage during COM-mode flight. Based on previous research, *R. nippon* is thought to primarily feed by perch hunting style, like *R. ferrumequinum* (Jones and Rayner, 1989), but future work is needed to determine what proportion of their feeding style is hawking, and whether they eat prey caught while stationary or on the move.

In addition, our data shows repeated visits to the same foraging site for all bats monitored in this study, except for bat D (Fig. 3, bat C_2 in Fig. 2B). When bats reached a foraging patch rich in prey, they searched intensively in the vicinity. In particular, the movement pattern of bat C_2 resembled a foray-search, a strategy for searching for foraging areas (i.e., flying away from a foraging area and returning to that area repeatedly in a foray-search pattern) (Conradt et al., 2000, 2003). The foray-search movement pattern is reportedly more efficient than a random walk when the targets are positioned in a uniform and clumped distribution (Conradt et al., 2003), and bats may use the foray pattern movement for such purpose while foraging.

Comparing all trajectories, only bat C_1, measured in September, flew almost directly northwest to the furthest distance away from the roost (Bat C_1 in Fig. 2A), suggesting that it may have flown for purposes other than foraging, as social behavior, for example. Furthermore, the ARB flight mode during the trip was relatively short for bat C_1 (Table 1), and the flight speed was higher than that recorded for other trips

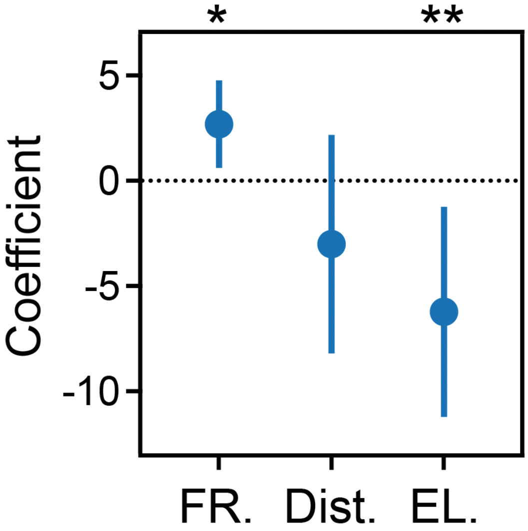

Fig. 6. The regression coefficients estimated by SSF modeling analysis for three variables: forest (left, FR), distance to roads (center, Dist), and elevation (right, EL). The categories of natural forests and conifer plantations are combined into a single covariate labeled "Forest": assigned a value of 1, while the other four categories (grassland, urban area, cropland, and water) were assigned a value of 0 because the bats primarily used the forest landscape (see Table 3). Vertical lines for each category represent the 95% confidence intervals. The asterisks indicate significance codes; ** $P < 0.01$, *$P < 0.05$. Bat D was excluded from this analysis because no valid burst was identified.

(see Supplementary Figure S2A). During this trip, there was no tailwind, and wind conditions were not largely different from those experienced by other tagged bats, suggesting that bat C1 was intentionally trying to move faster. Previous studies have reported that many insectivorous bat species, such as several members of genera *Myotis* and *Plecotus*, travel considerable distances and swarm at underground sites in late summer and autumn in temperate regions (Parsons et al., 2003; Rivers et al., 2006; Furmankiewicz et al., 2013) to mate (Kerth et al., 2003; Furmankiewicz and Altringham, 2007) and/or to assess potential hibernation sites. Although to date there is no evidence of swarming behavior by *Rhinolophus* species, it is possible that bat C_1 traveled a long distance because of unknown social behavior during the mating season.

In contrast, bat D moved continuously in a single area near the roost for over 4 h early at night (Fig. 2B). Interestingly, we visited this site and found that it was an area next to a pond with a relatively low tree density. The positions of bat D showed a Gaussian distribution in both the north-south and east-west directions (see Supplementary Figure S4), with a greater variation along the former compared to the variation from our error measurement when the stationary logger was installed at a single location within the forest (see Supplementary Figure S1). This result suggested that this data was not the result of a GPS logging error, but rather that Bat D remained there for an extended period of time as it moved within the foraging area near its roost. This behavior of bat D was presumably due to the weather, as it had been drizzling for nearly an hour during the GPS logging period.

Such differences in movement tactics related to foraging among individuals may be due to a variety of factors, including sex, weather, and season. However, further discussion is not possible at this time because of the small sample size. Nonetheless, this bio-logging study has shown previously unknown movement behavior during natural foraging of greater horseshoe bats, highlighting the importance and need for continued research on bat movement ecology in Japan.

Habitat use

A previous study conducted in the UK using radio telemetry found that *R. ferrumequinum*, which is a close relative of *R. nippon*, prefers to fly over pastures and forests (Duvergé and Jones, 2003; Flanders and Jones, 2009), whereas bats in western Europe prefer residential areas and meadow orchards (Dietz et al., 2013). On the other hand, forested areas account for 69% of the total area in the Iburi Region of Hokkaido, where the tracked bats in the present study flew (www.rinya.maff.go.jp); which is a higher percentage than the forested areas in the abovementioned studies (Duvergé and Jones, 2003; Flanders and Jones, 2009; Dietz et al., 2013). In this study, all bats including the two measured by pinpoint-50s predominantly occupied forested areas in both the ARB and COM flight modes, whereas pastures, meadows, orchards (categorized as grassland in this study), and residential areas were rarely visited by the bats. Additionally, altitude data from the GPS logger indicated that bats did not fly above the canopy but mainly within or under it. While previous studies have suggested that this bat species may exhibit flexibility in responding to the available habitat types in the landscape, our study showed the importance of forests among the habitats of this species. SSF modeling analysis indicates a preference for forest habitat by the bats. This was attributed to the suitability of forests for the perch-hunting foraging style exhibited by this bat species, given the abundance of tree branches. Additionally, *Rhinolophus* species generally have lower wing loading, which results in slow flight but good maneuverability (Norberg and Rayner, 1987). Flying within forests allows bats to avoid harsh weather and their predators. Moreover, forests are a major source of flying insects consumed by insectivorous bats.

Several previous studies using direct visual observation or infrared camera recordings also demonstrated that vespertilionid bats fly along fixed routes or so-called flyways, when commuting to foraging sites (Krull et al., 1991; Limpens and Kapteyn, 1991; Schaub and Schnitzler, 2007). Such a route-following behavior is one of the various large-scale navigation strategies of bats (Yovel and Ulanovsky, 2017). In this study, we found that *R. nippon* occasionally commuted along a forest road that was sufficiently wide for cars to pass on one side (Fig. 5C). Although it was clear that the bats followed the forest road, the SSF modeling analysis did not show that they prefer to fly close to the road. Instead, they significantly selected areas at lower elevations rather than higher elevations at each step (Fig. 6), suggesting that the bats prioritize easier movement at each stage rather than strict route-following. On the other hand, during route-following behavior, the bats tended to fly at right angles to the slope direction on relatively steep slopes (see Fig. 5B), indicating that they do not necessarily prefer low elevations.

This suggests that topographic features may play a more crucial role in habitat preference during movement than elevation alone. Also, for *R. nippon*, topographic features might serve as a more important navigational cue than roads. On the other hand, from the perspective of navigation through echolocation, the acoustic characteristics of returning echoes play an important role (Goldshtein et al., 2024). In this study, the echo characteristics are expected to be more pronounced on artificial roads than in natural topographic features. Because the ultrasound detection range of echolocating bats is shorter than the ranges of the visual sensory systems employed for navigation by other animals, such as birds, continuous echoes from the ground and from the left/right tree lines provide useful cues for creating local spatial maps for navigation. Further detailed investigation is needed to determine the extent to which *R. nippon* uses route-following behavior for navigation.

Ethical considerations

As bio-logging studies on wild echolocating bats have recently increased, data quality is likely to be prioritized under a trade-off between logger size and battery life, resulting in the use of data loggers weighing more than 10% of bats' body mass (Cvikel et al., 2015; Roeleke et al., 2016). Here, we limited the logger weight to a relatively small size, i.e., less than 10% of the body mass of the bats under study, although it is recommended to be less than 3%–5% of the body mass for flying animals, such as birds (Phillips et al., 2003) and bats (Aldridge and Brigham, 1988). A previous study showed that no significant differences were observed between the behavior of echolocating bats (*M. myotis* and *M. vivesi*) carrying loggers that were 15% of their body weight, and non-tagged individuals (Egert-Berg et al., 2018). The results reported herein showed that bats flew long distances at almost the same speed as reported in previous studies using radio telemetry (Aldridge, 1986; Tian and Schnitzler, 1997), suggesting that the influence of data logger weight on bat flight performance was negligible.

We should also consider how the stress caused by handling and logger attachments affects bat movement, as tagged bats might behave or move differently than usual and/or lose body weight. The results showed that the time at which the tagged bats emerged from their roosts was almost the same as previously reported (Funakoshi and Maeda, 2003). In addition, the body weight of bats with the attached data loggers, at the time they were recaptured after a couple of days, did not significantly decrease compared to that at the initial capture (see MATERIALS AND METHODS for details), lying within the range of body weight fluctuation observed in this bat species on a daily basis among the individuals reared in our laboratory. These observations suggest that extra loading from the logger had little effect on the nocturnal movements of *R. nippon*. Furthermore, we recaptured a female that had been investigated during pregnancy the previous year and did not find any damage. In this study, we caught and attached loggers to 27 bats. We only recaptured 10 bats (approximately 40% recapture rate) and succeeded in recovering the data from seven individuals. In previous studies, the recapture rate of the greater horseshoe bats which were tagged with small metal rings (several millimeters in diameter) was nearly 40% (Funakoshi and Maeda, 2003; Dietz et al., 2009). Therefore, the low recapture rate in this study was unlikely to be due to the extra load from the GPS data logger alone. However, the effects of logger attachment on the recovery rates of individuals and local populations have not been quantitatively assessed and data loggers will have to be smaller in the future to minimize the effects of extra loading. Regarding bat bio-logging studies, continued detailed observations and data accumulation are needed on the effects of logger attachment on bat behavior and health.

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COMPETING INTERESTS

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

EF and SH designed the study. EF, K. Yoshimura, TU, and DF performed the experiments. EF, K. Yoda, K. Yoshimura, and DF analyzed the data. EF, K. Yoda, DF, and SH wrote the paper. All authors gave final approval for publication.

SUPPLEMENTARY MATERIALS

Supplementary materials for this article are available online. (URL: https://doi.org/10.2108/zs230119)

Supplementary Text 1. Supplementary materials and methods.

Supplementary Figure S1. Positional distribution of GPS data loggers placed at three different sites within the forest near the bat roost.

Supplementary Figure S2. Mean values of step length **(A)**, turning angle **(B)**, and variations **(C)**; error bars in **(A)**, between two and three successive steps estimated by 2-state HMM, respectively.

Supplementary Figure S3. Mean value of step length **(A)**, turning angle **(B)**, and variations **(C)**; error bars in **(A)** between two and three successive steps estimated by 3-state HMM, respectively.

Supplementary Figure S4. Positional distribution of the GPS data logger that was attached to bat D (Fig. 2B).

Supplementary Table S1. Results of SSF modeling for COM-mode trajectory data of the bats.

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