Foraging activity and night-roost usage in the Japanese greater horseshoe bat, *Rhinolophus ferrumequinum nippon*

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**Abstract.** Nocturnal activity, foraging behavior and night-roost usage in *Rhinolophus ferrumequinum nippon* were examined using bat-detectors, radio transmitters and fluorescent tags. Emergence from the cave roost began around dusk from March to November. The mean emergence time averaged 14 min after sunset, and the principal foraging period was within a few hours after sunset. The main foraging style was flycatching (perch-hunting). The height of the branches used by bats as feeding or roosting sites averaged 4.1 m above the ground. The length of bat’s stay per feeding site averaged 6.6 min. In June, August and September, once the bats emerged, they seldom returned to the cave until just before sunrise, but in July, lactating females returned to the cave before midnight. In November, most of the bats returned to the cave about two hrs after sunset. Home range of adult females averaged 1.5 ha, and they foraged mainly in open forests, woodland paths or forest edges. The distances traveled to their main foraging sites averaged 0.87 km. Maximum-recorded distance traveled was 2.3 km during one night, and they hunted up to a distance of 2.0 km from the cave. Bats used specific night roosts, and their roosting bouts in the night roosts extended for about six hrs in April and varied from one to five hrs in June and October.

**Key words:** foraging behavior, home range, night-roost usage, nocturnal activity, *Rhinolophus ferrumequinum nippon*.

In previous papers (Funakoshi and Uchida 1978a; Funakoshi and Takeda 1998; Funakoshi and Fukue 2001), we investigated the hibernation, winter activity, diet, reproduction and growth in the Japanese greater horseshoe bat *Rhinolophus ferrumequinum nippon*. However, their nocturnal activity, foraging habitat and night-roost usage have not yet been examined in detail, except for the reports of Kuramoto (1972, 1977). Relatively few papers concerning the foraging behavior and nocturnal activity in rhinolophid bats have been published (Neuweiler et al. 1987; Jones and Rayner 1989; Jones and Morton 1992; Jones et al. 1995). Furthermore little is known about the seasonal changes in nocturnal activity of *R. ferrumequinum* (but see Jones and Morton 1992; Park et al. 1999, 2000). This species is an useful subject for such study, because its night roosting sites are easily accessible to observers. Furthermore, the above features are readily investigated by using bat-detectors, radio-tracking and banding. The present study was carried out to examine the nocturnal behavior and the use of night roosts. As a result of this research, we report the first information on the nocturnal activity and night roosting behavior in *R. f. nippon* and compare this with data from the same species in England and other species of bats.

**Study area and methods**

Principal investigations were made in and around the Katano-dō Cave in Kagoshima Prefecture (31°32’N, 131°10’E) from the spring of 1998 to the summer of 2001 (Fig. 1). The vegetation of this region consists of secondary laurel forests and coppice forests including *Quercus glauca, Castanopsis sieboldii, Lithocarpus*...
edulis and Cryptomeria japonica, with paddy fields (Fig. 2). A small brook flows near the entrance of the cave. The width of the entrance of the cave is about 7 m, and the length of its passage is about 70 m. Rhinolophus f. nippon, R. cornutus, Miniopterus fuliginosus, Myotis nattereri and Myotis macrodactylus were all found at the cave from spring to fall (Funakoshi and Takeda 1998). The inner part of the cave is very large, and was used as the maternity roost by R. f. nippon in summer. In order to investigate the total colony size, nocturnal and seasonal activities, we recorded the number of bats emerging each minute around sunset and the number of bats returning before sunrise at the entrance of Katano-dō Cave by using bat detectors (S-25 or Mini-3; Ultra Sound Advice, London, UK). In order to determine the flying routes, the bats flying out of the cave were counted at several points outside the cave by using bat detectors. These points were decided in order of distance from the cave based on the observations of the flights at various points in advance.

Flight paths, foraging sites and foraging or night-roosting behavior were observed by following bats fitted with chemiluminescent tags or radio tags, and with the use of bat detectors. The cylindrical fluorescent tags (37 mm, 0.5 g, on average 2% of bats’ body weight; Kemihotaru; Lumica Corporation, Koga, Japan) were attached to hair on their backs with instantaneous adhesive before release. Light from the tags lasted for approximately 6–10 hours. Due to this time period, 10–20 bats were captured by an insect net at the roost one hour before sunset. Sex and age were recorded, and bats were marked individually with flanged wing-bands, before being fitted with the tags at the entrance of the cave. Fluorescent light did not seem to disturb the bats in their feeding activity. Bats fitted with light tags were followed during eight nights in June–October 1998, four nights in June–August 1999, and one night in May 2000.

Home range and foraging site fidelity were investigated by radio-tracking. Three bats (adult females) were fitted with transmitters (1.2 g; Holohil Systems Ltd., Carp, Canada) which averaged 4.8% of the body weight of each bat. They were tagged at the entrance of the cave on 2 June 2001. Radio-fixes for perching bats were obtained by triangulation with three portable receivers (FT-290mk II; Vertex Standard Co. Ltd., Tokyo, Japan) at intervals of two hours for six nights in June–July 2001.
In order to investigate the movements in one night on the basis of banding-recapture method, other captured bats were also marked with wing-bands and then released at the entrance of the cave in 1998–1999. After that, other day-roosts were searched.

It was difficult to observe the night-roosting behavior after mid-night, because the power of fluorescence became weak. Therefore, it was desirable to find specific night roosts in order to examine their nonfeeding phases during the night. There were three outhouses used as night roosts by *R. f. nippon* at the second study area which was Satsuma-cho General Playground in Kagoshima Prefecture (31°55′N, 130°33′E) (Fig. 1). The distance between the outhouses A and B was about 100 m, and that between B and C was about 200 m (Fig. 3). Each outhouse had two separate rooms having one entrance each. Nocturnal observations using bat detectors and/or banding were carried out for nine nights in May–November 1998, one night in September 1999, one night in April 2000, and four nights in May–August 2002. In order to investigate use of night roosts, the presence of prey remains beneath roosts was examined, and number of feces for a night was counted in each room. In addition, their day roosts were searched in the study area. In the night roosts and day roosts, the ambient temperatures were measured at sites occupied by *R. f. nippon*.

Results

*Emergence time and flight direction*

At Katano-dō Cave, activity before sunset and lightsampling behavior were observed in *R. f. nippon*. Emergence began around dusk and continued for about 30 min after sunset from March to November (Fig. 4). The mean emergence time averaged 14 ± 1.7 (SE) min (range 2–22 min, n = 24) after sunset.

In June, *R. f. nippon* flew in every direction from the cave, but most of the bats flew rather low over the ground (1–2 m) and headed eastward. Of 20 bats carrying fluorescent lights, 14 (70%) flew to the east, and of 120 bats in the cave, 65 (54%) were counted at the east point by a bat detector (Fig. 5). In July, of 19 bats carrying fluorescent lights, 11 (58%) flew to the southeast, and of 220 bats that were counted at the entrance of the cave, 157 (71%) were counted at point A, while 49 (22%) were counted at point B. In August, of 20 bats carrying fluorescent lights, 4 (20%) flew to the southeast to point C, and of 117 bats in the cave, 40 (34%) were counted at the same point. In September, of 100 bats in the cave, 24 (24%) were counted at point D. Almost all the bats flew directly towards the southeast or east, and then gradually dispersed. The flight paths of *R. f. nippon* were situated in relatively open space.
Foraging behavior and nocturnal activity

*Rhinolophus f. nippon* emits pure tone frequencies. The constant frequency averaged 72 kHz, and the maximum distance that we could receive their echolocation sounds by using bat detectors was about 17 m. They hunted by flycatching and aerial hawking, but flycatching was more common. In flycatcher style, they emit sounds and detect insects from their perch. They then pursue and catch their prey and return to the same perch to eat it. The height of the perch used by the bats averaged 4.1 ± 0.32 (SE) m above the ground (range 2–10 m, n = 35). The length of their stay at the same perch averaged 6.6 ± 1.7 (SE) min (range 1–42 min, n = 25). The distance between the bats hanging on perches along the woodland paths averaged 103 ± 9 (SE) m (range 45–210, n = 31) in July and August 1998 and July 1999.

The active bats frequently echolocated, pursued and ate their prey at perches. The inactive bats, on the other hand, intermittently emitted feeble sounds while hanging on twigs and did not foraged. Each of the bats fitted with the light tags was counted at night. Out of the bats observed more than 90% were active within one hr after sunset (Fig. 6). But, three hrs after sunset, more than 70% of the bats became inactive (Fig. 6). Therefore, the principal foraging period was within a few hrs after emergence.

Changes in the return number at Katano-dō Cave are shown in Fig. 7. In June, all of the bats began to return to the cave one hr before sunrise. However, in the lactating season in July, flying activity became intermittent during the night, and most of the bats returned after mid-night. From late July to mid-September, they seldom returned to the cave until one or two hrs before sunrise. In October, some of the bats returned to the cave two hrs after midnight, but most of the bats began to return at about 5:00 am. In November 1998, most of the bats returned only about two hrs after sunset.

Of 15 lactating females fitted with fluorescent tags in
June 1999, 9 (60%) had returned one hr after sunset, and 14 (93%) had returned to the cave two hrs after sunset. Of 20 adult females fitted with tags in May 2000, 8 (40%) had returned four hrs after sunset, and 13 (65%) had returned to the cave five hrs after sunset.

Foraging areas and home ranges

The bats foraged mainly in open forests, woodland paths or forest edges (Fig. 2). They were not found in dense forests, open areas or near brooks. The adult females carrying fluorescent-tags foraged up to a distance of 2.0 km from Katano-dô Cave. Early in August, the newly weaned young foraged within 0.5 km of the roost, and sometimes returned to the roost together with their mothers at midnight. In the study area, four day-roosts were found around the Katano-dô Cave (Fig. 2). Maximum distance traveled was recorded as 2.3 km during one night on the basis of banding-recapture method at the day-roosts. Three bats (R1, R2 and R3) were tracked for six nights (Fig. 8). The greatest distances traveled by each radio-tracked individual were 1.98 km for R1, 0.48 km for R2 and 1.03 km for R3. The principal foraging areas, however, were widely separated. The distances traveled to such main foraging sites were 1.2 km for R1, 0.4 km for R2 and 1.0 km for R3, and the distances averaged 0.87 km. Minimum area convex polygons show the home ranges of the bats tracked during the summer (Fig. 8). In some areas, the home ranges overlapped each other. The home range sizes of R1, R2 and R3 were 2.7 ha, 0.6 ha and 1.2 ha, respectively, and the ranges averaged 1.5 ha ($n = 3$).

Night-roost usage

The bats began to enter the outhouses at Satsuma-cho General Playground to roost two hrs after sunset in April to early June and October (Fig. 9). From mid-June to September, however, they began to roost from three to five hrs after sunset (Fig. 9). Especially, from mid-June to July the period of usage was only about three hrs. Seasonal and nocturnal changes of the frequency of night-roost usage are shown in Fig. 10. In May, the number of bats roosting during the night had two peaks with the first one three hrs after sunset and the second one eight hrs after sunset (Fig. 10). Similar pattern was also shown in May 2002. In June, the number of roosting bats reached a peak about three hrs before sunrise. From June to September, such peaks were concentrated after midnight. In July, the number of bats roosting during the night was reduced (Fig. 10). In October, the bats started using the night roosts two hrs after sunset, and many of them began to leave the roosts four hrs after...
sunset (Fig. 10). On the other hand, in this season some of the bats began to return the Katano-dō Cave five hrs before sunrise (Fig. 7). In November, there were no bats in the outhouses at night.

Start of night-roost usage and roosting bout were varied with individuals (Fig. 11). Roosting bouts lasted for 1–5 hrs, and average duration of the bouts was 136 ± 21 (SE) min (n = 14) in early June (Fig. 11). In other seasons, roosting bouts lasted for three hrs in October 1998, and six hrs in April 2000. The total number of feces on the floors of the three outhouses reached 319 for a night in June, whereas those of feces decreased to 80 in September and 65 in October 1998. Similarly, 74 feces were found in September 1999. No prey remains beneath roosts were found in any season. The ambient temperatures at night-roosts by R. f. nippon ranged from 17 to 22°C in June, while those in day roosts ranged from 14 to 16°C.

During daytime searches, new 12 day-roosts were found around the playground (Fig. 3). Of 26 bats banded at the outhouses at night, 10 of them were recaptured at the two day-roosts (artificial caves). Thus, the distance traveled to the night roosts varied from 0.6–0.8 km.

Seasonal and nocturnal changes of the members of bats in each night-roost were shown in Fig. 12. In July, only one bat roosted in each room at different times after midnight, and three bats captured were adult males (Fig. 12). In August, of nine bats captured, all of them were adult females and young (Fig. 12). Their nursery colony, however, was not found around the night roosts at the study area. In September, of nine bats captured, seven were females, and only one adult male was found (Fig. 12). In room A1, four bats were found at the same time. In October, of 10 bats captured, six were adults and four were adult males (Fig. 12). Especially, in room A1 and C1, a pair of male and female was found respectively.

On the night of 18–19 September 1999, eight bats roosted in the outhouses (A1, A2, B2, C1 and C2), one of which was recaptured (F45 rested in room A1). On the night of 11–12 May 2002, six bats (two adult males, two adult females, one subadult male and one subadult female) roosted individually in rooms B1 and C1 at different times. One of them (adult male G83) was recaptured in room C1, and has since been captured in the same room in July and September 1998. On the night of 15–16 June 2002, five bats roosted in rooms A1, A2, B2, and C1 at different times. Three of them were adult males, one subadult female and the other one subadult male. The subadult male (F811) was recaptured in room C1, and has since been captured there on 12 May 2002. One owl (Strix uralensis) was observed near the outhouse (C1, C2) at 0:40 am on 16 June, 2002. On the night of 21 August 2002, three adult females and one
subadult female grouped in room C1, two of the adults were recaptured (F47 and F49). During the above study period, adult males were not found together in the same room.

Discussion

Foraging strategies

The emergence time in R. f. nippon approximately followed sunset (Fig. 4). On average, Rhinolophus f. nippon emerged about ten min earlier than Miniopterus fuliginosus, Myotis nattereri and Myotis macrodactylus, but about five min later than R. cornutus. Emergence at this time seems to be related with the appearance of insect prey, and with the feeding sites of relatively light open forests and with predation risk (Jones and Rydell 1994; Funakoshi and Takeda 1998). This idea is consistent with the smaller R. cornutus, which forages in darker dense forests, emerging earlier than R. ferrum-
equium. In addition, the flight paths of R. f. nippon were located in rather open spaces. Rhinolophus f. nippon is probably more susceptible to aerial predation than R. cornutus. On the other hand, M. fuliginosus which hunts in open spaces far above the woodland canopy emerged later than the other species. Miniopterus fuliginosus may avoid the risk of predation by diurnal or nocturnal predators in the sky.

The flight paths of the emerging bats were evidently specific. They flew rather low above the ground (1–2 m), as stated also by Ransome (1990). Most of the bats flew directly toward the southeast or east (Fig. 5). In these directions, there were densely distributed foraging sites (Fig. 2). In addition, they repeatedly used certain foraging areas. It seems that their food supply distribution was patchy in space over the study area.

Foraging in flycatcher style presented here is consistent with a previous field study of R. ferrumequinum (Jones and Rayner 1989), and is similar to that in relatively small Rhinolophus rouxi (Neuweiler et al. 1987). Rhinolophus ferrumequinum sometimes hunts by aerial hawking: bats detect, pursue and eat their prey on the wing (Kuramoto 1972; Funakoshi 1978; Jones and Morton 1992; this study), or by ground gleaning: landing on the ground and catching flightless insects (Stebbings 1977). It is conceivable that R. ferrumequinum is flexible in its foraging style according to habitat.

Jones and Rayner (1989) suggested that flycatching evolved in species feeding on large insects that the bats find difficult to handle during flight. Relatively large Megadermatid bats forage in flycatcher style (Vaughan and Vaughan 1986; Norberg and Rayner 1987). Many of them perch on low branches and listen for ground-dwell-
ing prey (Vaughan 1976; Fiedler 1979). The smaller lesser horseshoe bat (R. hipposideros), in contrast, is predominately an aerial hawker (Jones and Rayner 1989). Large insects generally occur at lower densities, and the energetic cost of perching and waiting for large prey may be considerably lower than continual flying while hunting.

The principal foraging period was within a few hrs after sunset, and was followed by resting bouts (Fig. 6). Similar activity has been shown in R. ferrumequinum in England (Jones and Morton 1992) and in R. rouxi in Sri Lanka (Neuweiler et al. 1987). In addition, one or two short foraging bouts were shown between midnight and sunrise (Jones and Morton 1992). Rhinolophus f. nippon probably forage on their way from night roosts to day roosts just before sunrise in our study areas. In any case,
such a foraging pattern appears to be closely correlated with the emergence of insect prey, as shown in *M. fuliginosus* (Funakoshi and Uchida 1975) and *P. abramus* (Funakoshi and Uchida 1978b). In addition, seasonal dietary shifts and food choice was consistent with the changes of food conditions throughout the year (Funakoshi and Takeda 1998).

Greater horseshoe bats foraged mainly in open forests, woodland paths or forest edges, and were not found in dense forests, open area or over brooks (Fig. 2). At Akiyoshi-dai Plateau, they foraged also over the river or above the grassland (Kuramoto 1972). In England, many *R. ferrumequinum* are found in patches of trees where they hunt by flycatching (Jones and Rayner 1989). They forage in ancient woodland during the spring, and over pasture containing trees during late summer (Jones and Morton 1992). The seasonal shift in habitat use may be associated with the seasonal changes in food abundance and prey (Jones 1990; Jones et al. 1995). In contrast, *R. rouxi* forage only in dense forest and are not found in open woodland in October (Neuweiler et al. 1987). For *R. f. nippon*, the flexible food choice (Funakoshi and Takeda 1998) and the foraging site selection mentioned above may well fit in with the seasonal changes of food availability in warm-temperate regions.

In the study area, the adult females foraged up to a distance of two km from the cave, which was much shorter than that of the same species in England (5 km; Jones and Morton 1992). Such short distances in our study area may be associated with the distances traveled from the day roosts to feeding areas, or with abundance of food resources around the day roosts. The newly weaned young foraged up to distances of 0.5 km, similar to those reported in the same species (Jones et al. 1995). Mother and young frequently leave the day-roost together in the flying stage (Matsumura 1988), but during weaning the development of foraging behavior in *R. ferrumequinum* involves no tuition from the mother, and young forage independently of their mothers (Jones et al. 1995).

The home ranges of individuals overlapped each other to some extent, but each principal foraging site that was repeatedly used was separate (Fig. 8), and bats hanging from trees were widely spaced along the woodland paths. We observed no territorial behavior at foraging sites, however, and thus, it seems that *R. f. nippon* has no clear feeding territory, as stated by Jones and Morton (1992). They may avoid the struggle for defending food by spacing. *Rhinolophus rouxi*, perch on specific twigs, hunt in flycatcher style and its foraging areas are not defended against intruders (Neuweiler et al. 1987).

**Use of night roosts**

The timing and duration of nightly rest periods vary with seasons, according to ambient temperature, reproductive condition and prey availability (Kunz 1982). In this study, the bats began to use the night roosts around foraging sites or day roosts two hrs after sunset in spring (Fig. 9). In some cases, the duration of roosting bouts at night lasted for six hrs in April. Most of the bats returned to their day roosts before midnight in May. Such short feeding bouts may be closely related to shortage of prey for *R. f. nippon* including large Coleoptera and Diptera during this season (Funakoshi and Takeda 1998).

In summer, once the bats emerged at sunset, they seldom returned to the cave until one or two hrs before sunrise, except for lactating females early and mid-July. Most of the bats became inactive on a perch three hrs after sunset (Fig. 6). Roosting bouts during the night roosts varied from one to five hours (Fig. 11). Nocturnal flying insects were most abundant in June and July (Funakoshi and Takeda 1998), and in this season, the feces on the floor of the outhouses at Satsuma-cho General Playground were great in number. Thus, in summer most of the bats may forage or roost on a perch intermittently during the night, and not frequently use night roosts.

In all of the outhouses, prey remains were not found beneath roosts. The results indicate that the outhouses are exclusively used as roosting places at night, and do not serve as masticating sites like feeding perches. Warmer ambient temperatures of the night roosts may promote the digestion of food or absorption of nourishment, as stated by Kunz (1982). In addition, if night roosts are within easy reach of the feeding sites, the cost of the movement between them may be reduced. Night roosts may also act as protection from predators, such as owls (Kuramoto 1977).

In July, in the breeding season, lactating females had short foraging bouts just after sunset, and most of them had returned to the nursery cave by two hrs after sunset. After that, they embraced infants until sunrise (Sano 2000; Funakoshi and Fukue 2001). As a result, lactating females did not use night roosts. Only adult males were captured at the night roosts after midnight in July (Fig. 12), and some of them were recaptured in September and October. It is possible that adult males change their night roosts seasonally, and do not defend these roosts.
for extended periods in summer. Adult males were always solitary in night roosts, and a few used the same roost repeatedly. In August, the night roosts were occupied by the postlactating females and their young. In September, subadult females and adult males began to use the night roosts, together with the adult females and young (Fig. 12).

In October, the bats used night roosts from about two hrs after sunset, and began to return to their day roosts five hrs before sunrise (Figs. 7 and 9). Possibly, they use night roosts or day roosts for many hours at night when feeding is unproductive in this season. As stated by Anthony et al. (1981), long night roosting periods and short foraging periods are associated with cool nights and low prey density. In the mating season, a pair of adult male and female was found in October (Fig. 12). It is probable that night roosts may be used as a mating place late in autumn. In November, the bats only used the night roosts for a short period and returned to their day roosts about two hrs after sunset. They considerably restrained their activity in this season, as in M. fuliginosus (Funakoshi and Uchida 1975) and P. abramus (Funakoshi and Uchida 1978b).

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