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Does communal nesting help thermoregulation in Japanese flying squirrels (*Pteromys momonga*) in winter?

Hayato Kikuchi, Shigeyuki Izumiyama & Tatsuo Oshida*

ABSTRACT. Communal nesting is suggested to assist with thermoregulation in tree squirrels and flying squirrels in temperate and subarctic zones during winter. We tested the thermoregulation hypothesis as an explanation for the ecological function of communal nesting in Japanese flying squirrels (*Pteromys momonga*). We observed their nesting behavior using video camera traps. *Pteromys momonga* is endemic to Honshu, Shikoku, and Kyushu, Japan. The study was conducted from December 1, 2017 to November 30, 2019 in the northern part of the Kiso Mountains, Nagano Prefecture, Japan. During the snowy season, the number of flying squirrels nesting in a cavity varies daily. The fluctuation in the daily maximum number of individuals nesting communally did not correlate with ambient temperature, suggesting that communal nesting may not always be related to thermoregulation.

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Hayato Kikuchi [s19180001@st.obihiro.ac.jp] and Tatsuo Oshida, [oshidata@obihiro.ac.jp], Laboratory of Wildlife Biology, Obihiro University of Agriculture and Veterinary Medicine, Inada, Obihiro 080-8555, Japan; Shigeyuki Izumiyama [izumiys@shinshu-u.ac.jp], Institute of Mountain Science, Shinshu University, Minamiminowa, Kamiina-gun 399-4511, Nagano, Japan.

Помогает ли совместное гнездование японских белок-летяг (*Pteromys momonga*) их терморегуляции зимой?

Кикучи Х., Изумияма Ш., Ошида Т.*

РЕЗЮМЕ. Предполагается, что совместное гнездование способствует терморегуляции в зимний период у белок и белок-летяг в умеренных и субарктических зонах. Мы проверили гипотезу терморегуляции как объяснение экологической функции коллективного гнездования у японских белок-летяг (*Pteromys momonga*). Мы наблюдали за их гнездовым поведением с помощью видеоловушек. *Pteromys momonga* является эндемиком Японских островов — Хонсю, Сикоку и Кюсю. Исследования проводились с 1 декабря 2017 г. по 30 ноября 2019 г. в северной части гор Кисо, префектура Нагано, Япония. В снежный период количество летяг, собирающихся в дупле, меняется ежедневно. Колебание суточного максимального количества особей, гнездящихся сообща, не коррелировало с температурой окружающей среды, что позволяет предположить, что совместное гнездование не всегда может быть связано с терморегуляцией.

КЛЮЧЕВЫЕ СЛОВА: фотоловушка, гнездовое убежище, терморегуляция.

Introduction

Nesting is an important survival behavior in rodents; the nest protects them against predators and competitors (e.g. Lewarch & Hoekstra, 2018). Sciurids exhibit two types of nesting behavior: social (communal) nesting and asocial (solitary) nesting. Communal nesting occurs in some ground-dwelling squirrels, such as the cape ground squirrel *Xerus inauris* (Waterman, 1995) and black-tailed prairie dog *Cynomys ludovicianus* (Hoogland, 1996). These squirrels form colonies consisting of many individuals. Solitary nesting is usually found in many arboreal squirrel species, such as the Indian giant squirrel *Ratufa indica* (Pradhan *et al*., 2017) and the Japanese giant flying squirrel *Petaurista leucogenys* (Kawamichi *et al*., 1987).

Squirrels that typically show solitarily nesting do occasionally exhibit communal nesting. Communal nesting has been documented in tree squirrels of the genera *Sciurus* (Halloran & Bekoff, 1994; Koprowski, 1996; Edelman & Koprowski, 2007) and *Tamiasciurus* (Ramos-Lara & Koprowski, 2012; Williams *et al*., 2013).

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* Corresponding author

Communal nesting has also been documented in flying squirrels of the genera *Glaucomys* (Stapp *et al*., 1991; Layne & Raymond, 1994; Reynolds *et al*., 2009) and *Pteromys* (Kobayashi, 2013; Selonen *et al*., 2014; Asari & Yanagawa, 2016). Many authors have suggested that occasional communal nesting by tree squirrels and flying squirrels in temperate and subarctic zones during winter assists their thermoregulation (Layne & Raymond, 1994; Edelman & Koprowski, 2007; Garroway *et al*., 2013; Williams *et al*., 2013). Huddling effectively decreases metabolic heat production and maintenance costs in small rodents such as the bank vole *Myodes glareolus* (Gębczyński & Gębczyński, 1971) and deer mouse *Peromyscus maniculatus* (Andrews & Belknap, 1986).

To test the thermoregulation hypothesis, we examined the relationship between the nesting behavior of the Japanese flying squirrel *Pteromys momonga* and minimum ambient temperature. This squirrel is an arboreal species and nests in tree trunk cavities (Koprowski *et al*., 2016); it is usually asocial, but can nest communally in early spring, autumn, and winter (Kobayashi, 2013). *Pteromys momonga* is endemic to Honshu, Shikoku, and Kyushu islands of Japan, inhabiting montane coniferous forests (Koprowski *et al*., 2016). Compared to the northern areas of the Eurasian Continent, where *Pteromys volans* is widely distributed (Koprowski *et al*., 2016), the ambient temperature of these three islands is warmer because they are located in a lower latitude. Therefore, we aimed to test whether communal nesting is less common on these islands, as the temperature is warmer. If the thermoregulation hypothesis is correct, communal nesting should be limited to colder days (probably intermittently) in winter. Kobayashi (2013) previously suggested that thermoregulation may be a reasonable factor in communal nesting, but his study was inconclusive. If a few *P. momonga* nest together at higher ambient temperatures, thermoregulation may not be the primary reason for communal nesting. Primarily, we aimed to test whether thermoregulation is the main factor prompting communal nesting in *P. momonga*. We examined the relationship between minimum ambient temperature and the number of individuals nesting communally during the snowy season. In addition, we observed whether the members nesting communally separated temporarily on relatively warm days, even during the snowy season.

Materials and methods

Study area

The study was conducted in the northern part of the Kiso Mountains (1000–1200 m above sea level) in Nagano Prefecture (35.85° N, 137.93° E), Japan (Fig. 1). The forest vegetation in the study area was dominated by the Japanese cedar *Cryptomeria japonica*, Japanese cypress *Chamaecyparis obtusa* and larch *Larix leptolepis*. The forest was mainly plantation. The mean annual air temperature ranged from 11.8° to 12.9°C. The hottest months were from July to August when the mean monthly maximum air temperature ranges from 30.9° to 32.6°C. The coldest month was January, with a mean monthly minimum temperature ranged of –5.1° to –5.8°C. The annual precipitation ranged from 1143.5 to 1701.0 mm. The meteorological data for this area are available in the database of the Ina National Meteorological Station, which was 8 km away from the study area (Japan Meteorological Agency, 2020).

Preliminary survey

We randomly searched for tree cavities that were potential nests for *P. momonga* in the study area from October 2016 to December 2017. From April 2017 to December 2019, we confirmed the use of tree cavities as nesting sites for *P. momonga*. We visually observed the cavities for 1 h after sunset and/or 1 h before sunrise. We observed the cavities from a distance of approximately 15 m to avoid potentially disturbing the occupants. If *P. momonga* used the cavity, we counted the number of individuals using the cavity by direct observation. This survey identified five cavity nests in the trunks of the Japanese cedars and one in the Japanese cypress.

Camera trap survey

To investigate seasonal changes in the numbers of communally nesting flying squirrels, we observed nests using video camera traps with infrared motion sensors and infrared LED lights (Trophy Cam, Bushnell, Kansas, USA) for 2 years, from December 1, 2017 to November 30, 2019. Of the cavity nests identified through the field survey, three nests (A and B on the trunk of Japanese cedar and C on the trunk of Japanese cypress) enabled the camera traps to be placed within 3–5 m. Thus, we monitored three cavity nests in this study. The distances between nests A and B, A and C, and B and C were approximately 50, 275, and 320 m, respectively. The heights of nests A, B, and C were approximately 8, 4, and 5 m from the ground, respectively. A camera trap was placed in front of each nest using a belt. Each camera trap recording was 60 sec. We set the interval between recordings to 0 sec. To reinforce the camera trap survey, we occasionally visually observed the nests for 1 h after sunset and/or 1 h before sunrise.

Data analysis

We identified the animal species in each video and recorded the dates and times. For each nest cavity, we treated the maximum number of flying squirrel images taken by the camera trap from 30 min before sunset to 90 min after sunset as the daily number of flying squirrels nesting communally. We confirmed that *P. momonga* consistently left the nest cavity within the time range identified in the preliminary survey.

To evaluate the relationship between minimum ambient temperature and the number of flying squirrels nesting communally, we compared the minimum ambient temperatures with an individual nesting solitarily and those with individuals nesting communally at one nest on the same day using the Mann-Whitney's *U*-test. Here,

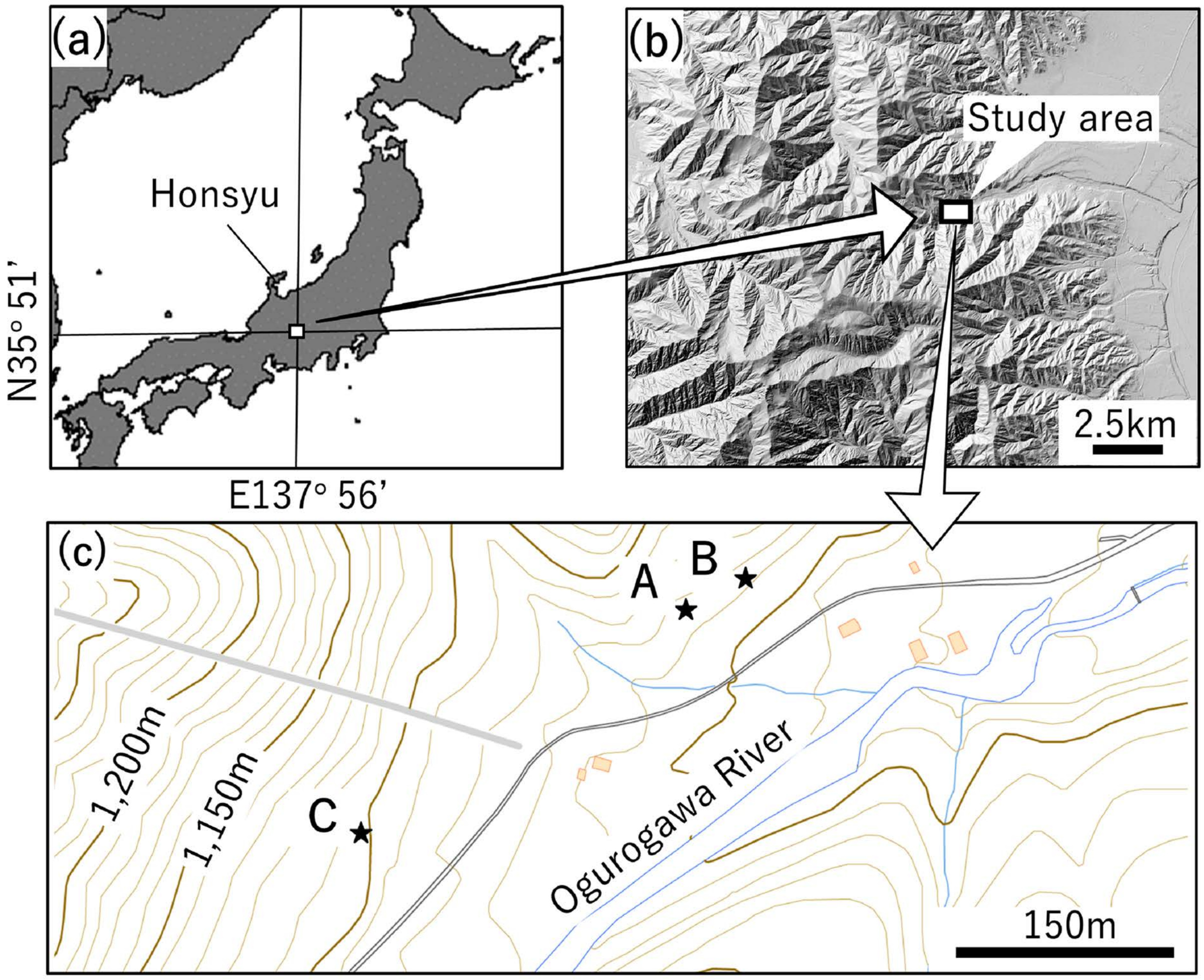

Fig. 1. Study location in the northern area of the Kiso Mountains (1000–1200 m above sea level), Nagano, Japan (a and b); stars indicate study sites A, B, and C (location of cavity nests of *Pteromys momonga*) established in the present study (c).

when a single *P. momonga* used one or more nests, we defined the individual as “nesting solitarily”; when *P. momonga* used communally at least one nest, we defined them as “nesting communally”.

Previous reports suggest that *P. momonga* mothers are likely to nest together with their offspring from spring (late March) to autumn (early November) (Torii, 1989; Yanagawa *et al*., 1996; Kobayashi, 2012; Oshida, 2015). This nesting behavior is essentially different from the communal nesting of adults. Therefore, we excluded communal nesting of mothers with offspring by restricting the data collection from December to March (i.e., outside the offspring rearing phase).

As each *P. momonga* individual is thought to have a settled home range (Kobayashi, 2012), we considered that they may not have immediately formed a large communal nesting group, but do it gradually, as it becomes cooler. To assess the effect of fluctuating daily temperatures (warmer or cooler) on the numbers of communal nesting, we recorded fluctuations in the maximum number of individuals nesting communally for two successive days. As nests A, B, and C were located close to each other, it was difficult to avoid the effect of spatial autocorrelation. Therefore, we identified the highest number of individuals among the three nests, as the maximum number of individuals on the day. We categorized the temperature data into three cases: “increase” (1°C or higher than the previous day), “decrease” (1°C or lower than the previous day), or “no change” (same as the previous day). We analyzed the “increase” and “decrease” data. In addition, we categorized the data from the maximum number of individuals into three cases: “increase” (more than the previous day), “decrease” (less than the previous day), or “no change” (same as the previous day). From spring to autumn, we considered that any effect of temperature fluctuation could be irrelevant because the temperature is within the usual range of thermal tolerance for *P. momonga*. Therefore, we examined the maximum number of individuals nesting in the snowy season (December, January, February, and March) using Fisher’s exact test. Temperature data were obtained from the Ina

National Meteorological Station (Japan Meteorological Agency, 2020). All statistical analyses were performed using the base and coin packages (Hothon *et al*., 2008) in software R ver. 3.6.2 (R Core Team, 2019).

Results

Visual observations

From October to December 2019, we confirmed that the number of squirrels using a nest cavity ranged from one to nine, showing a highly variable group size (Fig. 2). The numbers of individuals detected in nests A, B, and C were 0–3, 0–4, and 0–9, respectively.

Camera trap survey

We obtained behavioral data on communal nesting using three camera traps on nests A, B, and C. Unfortunately, faulty cameras prevented us from obtaining the data for nest A from January 4 to 12, 2018, for nest B from November 25 to December 12, 2017 and for nest C from December 1, 2017 to January 21, 2018 and from March 14 to July 22, 2019. *Pteromys momonga* was recorded in 2559 videos for 1981 trap nights. The camera at nest A recorded 1093 videos on 721 trap nights. The camera at nest B recorded 988 videos on 712 trap nights. The camera at nest C recorded 478 videos on 548 trap nights. Of these, communal nesting was recorded in 97, 60, and 27 videos (nights) at nests A, B, and C, respectively.

From December 2018 to March 2019, the minimum ambient temperatures were not significantly different between cases with solitary nesting squirrels (n = 36) and those with communally nesting squirrels (n = 56) (Mann-Whitney's U-test: Z = –0.65; p = 0.74) (Fig. 3). Moreover, in the snowy season, fluctuations in daily temperature did not significantly affect the maximum number of nesting individuals (Fisher's exact test: p = 0.48; Tab. 1). The data varied in some months; we showed a relationship between temperature fluctuations and the maximum number of individuals in the top three months (December 2018 to February 2019) (Fig. 4). We concluded that fluctuations in daily temperature were unlikely to affect the number of nesting individuals.

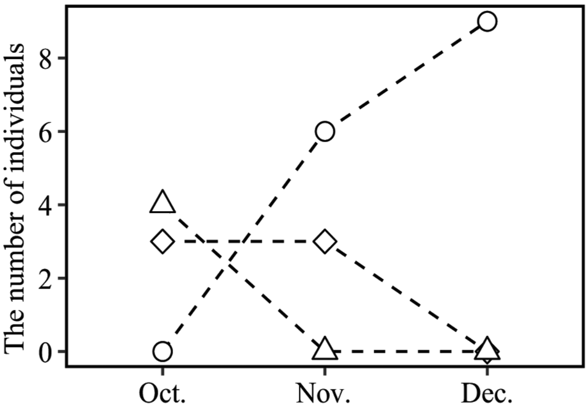

Fig. 2. The number of *Pteromys momonga* nesting communally from October to December 2019. Open diamonds, open triangles, and open circles indicate nests A, B, and C, respectively.

Other behavior

Additionally, we observed five instances of mating behavior near nests A and B in January and/or February. In two instances, we recorded that the communally nesting members copulated with each other: nest A on February 14, 2018 and nest B on February 13, 2019 (Fig. 5).

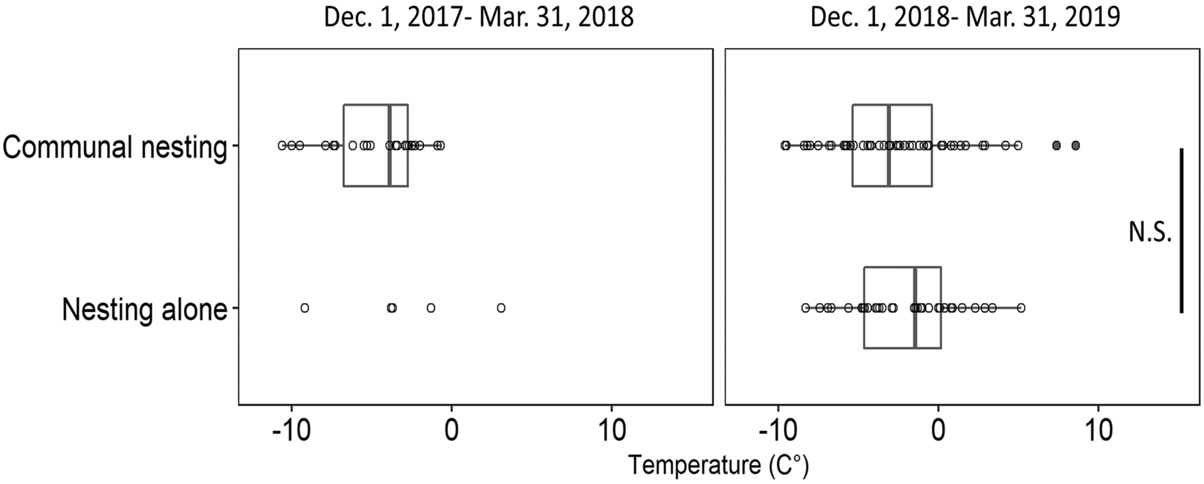

Fig. 3. Comparison of the daily minimum temperatures between cases with an individual nesting alone and those with highest number of individuals nesting communally (either A, B, and C) over winter in 2018 and 2019. N.S. indicates that the difference was not statistically significant (Mann-Whitney's U test).

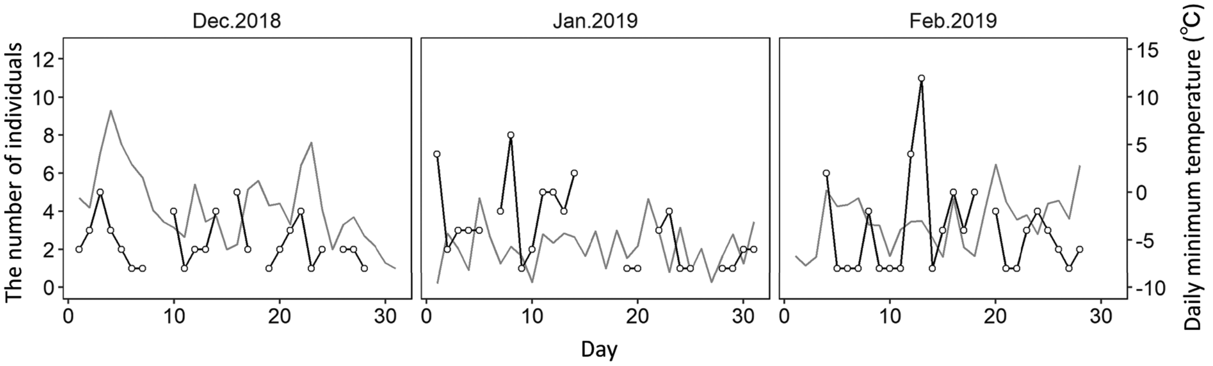

Fig. 4. Relationship between daily minimum temperature (gray lines) and the maximum number of *Pteromys momonga* nesting communally in one of three nests (A, B, and C). We selectively present the monthly data with the highest three numbers of individuals nesting together for each nest. Open circles and bold lines indicate fluctuations in the number of squirrels between two successive days.

Table 1. Fluctuation in the maximum number of *Pteromys momonga* in one of the three nests observed in two successive days: the fluctuation cases were recorded as three alternatives: increase, decrease, or no change. Fluctuation in temperature defined as + (1°C or higher than previous day) and – (1°C or lower than previous day).

Month	Fluctuation in temperature	Number of cases		
		Increase	No change	Decrease
December	+	5	0	3
	–	2	2	4
January	+	2	4	2
	–	5	2	0
February	+	3	1	1
	–	3	2	4
March	+	4	0	2
	–	3	4	3
Total	+	14	5	8
	–	13	10	11

Discussion

Our results did not support the hypothesis that communal nesting is associated with thermoregulation. Although we suspected that the number of individuals nesting in a cavity might be affected by daily temperature fluctuations during the snowy season, we did not find a clear relationship between the maximum nesting numbers and temperature (Tab. 1 and Fig. 3). This suggests that changes in ambient temperature do not affect the group size of communal *P. momonga* nests. In the present study, we observed that *P. momonga* often nested alone, even during the snowy season. Thus, colder temperatures may not always prompt for *P. momonga* to start communal nesting. Many studies have suggested that communal nesting functions as a form of thermoregulation for small mammals in cold weather (Layne & Raymond, 1994; Edelman & Koprowski, 2007; Garroway *et al.*, 2013; Williams *et al.*, 2013). Huddling by small mammals is thought to reduce energy requirements under cold conditions (e.g. Vogt & Lynch, 1982; Andrews & Belknap, 1986). Stapp *et al.* (1991) reported that six southern flying squirrels *Glaucomys volans* huddling in a wooden nest box in New Hampshire reduced their energy expenditure by 36% at a temperature of 9°. Unlike *G. volans*, *P. momonga* may efficiently maintain energy without requiring a huddling effect. During winter, *G. volans*

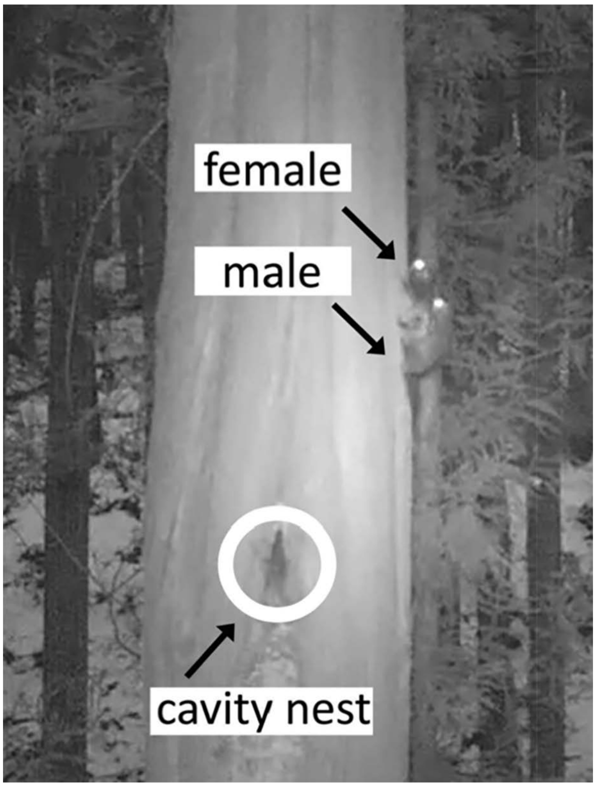

Fig. 5. Copulation behavior by the communal nesting members in *Pteromys momonga* recorded on February 14, 2018.

faces a food shortage because of its granivorous feeding habits (Muul, 1968; Harlow & Doyle, 1990) and undergoes periodic torpor (Muul, 1968). Therefore, huddling could effectively help save energy. *Pteromys momonga*, however, does not become torpid during winter. Although the feeding habits of *P. momonga* remain unclear, this species is thought to be both granivorus and folivorous (Oshida, 2015). In winter, *P. momonga* eat leaves and buds, whereas *P. volans* in Hokkaido (Japan) eat buds of *Alnus japonica* and *Betula platyphylla* during winter (Yanagawa, 1999). Compared to *G. volans*, *Pteromys* species may be better adapted to cold environments.

In the present study, we observed that members nesting communally copulated with each other twice. Communal nesting members may opportunistically copulate with several individuals. Yanagawa (1999) reported that a nesting pair of *P. volans* attempted to copulate immediately after leaving the nest in Hokkaido (Japan). Selonen *et al*. (2014) also reported that in Finland, a female first copulated with a male from the same nest before mating with individuals from other nests within a single night. The communal nesting of *P. volans* is likely to be primarily motivated by breeding in Hokkaido, Japan (Asari & Yanagawa, 2016). The present study confirmed two cases of mating between members of the same nest, but it is difficult to conclude that communal nesting is advantageous for reproduction.

We tested the thermoregulation hypothesis to clarify the ecological function of communal nesting in the usually asocial *P. momonga*. We could not confirm that communal nesting by *P. momonga* was not due to thermoregulation from the present data. Further studies should test the breeding hypothesis to clarify the ecological function of communal nesting in *P. momonga*.

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