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Regional differences in winter activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*) from Korea

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Abstract

Background: Hibernating bats exhibit ubiquitous winter activity in temperate zones, but there is considerable between- and within-species variety in their intensity and purpose. Bats may fly during winter for sustenance or travel to other hibernacula. This study compared inter-regional variation in the winter activity of the greater horseshoe bat (*Rhinolophus ferrumequinum*). We predicted that weather and hibernacula-environmental conditions would influence winter activity patterns.

Results: Winter activity patterns differed between regions. In the Anseong area, we confirmed movement inside the hibernaculum, but in Hampyeong, we observed movement both inside and between hibernacula. The two regions differ by 4 °C in average winter temperatures. Anseong experiences 22 days during which average daily temperatures exceeded 5 °C, whereas Hampyeong experienced 50 such days. During the hibernating period, bat body weight decreased by approximately 17–20% in both regions.

Conclusions: Ambient temperatures and winter-roost environments appear to be behind regional differences in hibernating bat activity. As winter temperatures in Korea do not favor insect activity, feeding probability is low for bats. However, bats may need to access water. At Anseong, underground water flows inside the hibernaculum when the reservoir outside is frozen. At Hampyeong, the hibernaculum does not contain a water source, but the reservoir outside does not freeze during winter. In conclusion, water-source location is the most likely explanation for regional variation in the winter activity of hibernating bats.

Keywords: Cave-dwelling bat, Hibernation, *Rhinolophus ferrumequinum*, Temperature, Winter activity

Background

Hibernation is an energy-saving mechanism to facilitate survival over a period with low temperatures and resources (Thomas et al. 1990; Humphries et al. 2003; Kokurewicz 2004; Geiser 2013). However, hibernation has significant ecological and physiological costs (Thomas et al. 1990; Thomas 1995; Speakman and Rowland 1999; Geiser and Brigham 2000; Park et al. 2000; Humphries et al. 2003; Geiser 2006), so hibernating species require a sophisticated strategy in response to fluctuating winter environments (McNab 1974; Webb et al. 1996).

Numerous bat species hibernate (Whitaker and Rissler 1992; Geluso 2007), but interestingly, hibernating bats are known to awaken from torpor and leave their hibernacula to restore a physiological imbalance (Ransome 1971; Willis 1982). Indeed, bats residing in temperate zones are ubiquitous in exhibiting winter activity, flying inside and outside of roosts, or switching between hibernacula (Whitaker and Rissler 1992). These periodic arousals can cost animals up to 80% of their energy stores (Thomas et al. 1990).

Because of the expense of such activities, researchers are interested in their exact function. Bats may fly outside during winter to feed, drink, or move to other hibernacula (Ransome 1968; Tidemann and Flavel 1987; Willis 1982; Speakman and Racey 1989; Thomas and Cloutier 1992). Until recently, the principle explanation for winter arousals from torpor was to avoid starvation (Ransome 1968; Avery 1985; Whitaker et al. 1997; Park et al. 1999), as emergence is consistent with a strategy of maximizing

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net energy gain (Avery 1985). Several studies have identified a correlation between emergence behavior and external temperature (Ransome 1968; Park et al. 1999; Arlettaz et al. 2000; Geluso 2007; Turbill 2008), supporting the hypothesis that winter activity is associated with achieving energy balance.

As water is a more vital resource than food during hibernation, obtaining sufficient water is another proposed reason for winter emergence (Speakman and Racey 1989). Observational and mist-netting research of several bat species in New Mexico provided evidence of winter drinking and feeding (Geluso 2007). Other competing explanations for bat winter activity include physiological or immune function responses. Attempts to develop a broadly applicable hypothesis have proven difficult because there is considerable within- and between-species variation in activity intensity and apparent purpose (Ransome 1968; Avery 1985; Whitaker and Rissler 1992; Park et al. 1999; Luis and Hudson 2006; Boyles et al. 2006; Geluso 2007; Turbill 2008; Ben-Hamo et al. 2013).

This study examined winter activity in greater horseshoe bats (*Rhinolophus ferrumequinum*) of South Korea. We predicted that winter activity would differ between regions in accordance with variation in environmental and weather conditions. We compared winter activities of bats in the southern and central regions of the Korean peninsula differing in winter temperatures both inside and outside the hibernacula. Based on our results, we aimed to explain why *R. ferrumequinum* would awaken from hibernation to engage in energetically costly behavior.

Methods

Study species

Rhinolophus ferrumequinum is a wide-ranging species found in North Africa, southern Europe, southwest Asia, the Caucasus, Iran, Afghanistan, Pakistan, the Himalayas, south-eastern China, Korea, and Japan (Csorba et al. 2003). In South Korea, the bat is broadly distributed widely and hibernates in underground sites that experiences large temperature fluctuations (1–15 °C) during winter (Kim et al. 2014). In several sites, hibernating bats are commonly found at temperatures ranging from 1 to 15 °C in caves and mines, and from solitary individuals to clusters containing several hundred individuals (Kim et al. 2014). *R. ferrumequinum* had more broad-ranged thermal preference for the hibernation site than other cave-dwelling bats in Korea (Kim et al. 2014).

Study sites

Bat activity was tracked in two abandoned mines in Anseong (central Korea) and five in Hampyeong (southern Korea) from December to March of 2007 and 2008 (Fig. 1).

These mines had been established in early 1900 to exploit gold or copper, but all mining activities ceased at the beginning of the twentieth century. At Anseong, the Sanpyeong mine has one entrance (height, 1.5 m; width, 2 m) and consists of a 350-m-long main passage and a 100-m-long side passage. Passage size is generally 2 m × 2 m, and some sections have a vertical passage with a 10-m ceiling. The Daemyeong mine also has one entrance (height, 2 m; width, 1.8 m), with a 65-m main passage and a 2.5 × 3 × 5-m side passage, 2.5-m high height, and 3 m wide. In both mines, groundwater flows from the entrance to the interior of the main passage during winter. The two hibernacula are 7.7 km apart, as well as 2 km and 3 km from the nearest reservoir, respectively (Fig. 1).

At Hampyeong, the Jucjang mine has one entrance and one main passage of dimensions 55 m × 2 m × 2.5 m (length × height × width). The Myodong mine has one entrance (1.8 m height × 2 m width), a 35-m main passage ending in a broad gallery (5 × 5 m), and a 15-m side passage. The Songsan mine has one entrance and a 90-m main passage (2 m height × 2.5 m width); 30 m straight inward from the entrance is a domed room (3.5–4.5 m height, 4–2.5 m width). The Jeongchang mine has one entrance (1.8 m height × 1.7 m width), one 85-m main passage, and two side passages (15 m and 26 m long, both 1.8 m height × 2 m width). Finally, the Deokyang mine has an entrance, a 97-m main passage, and two side passages (8 and 12 m long); entrance and passage dimensions are both 1.7 m wide and 1.8 m tall. None of the mines had standing water, but a reservoir is located 1 km away. The shortest distance among these five hibernacula is 1–20 km; Jucjang and Myodong are close together, while Songsan, Jeongchang, and Deokyang are close (Fig. 1). Observers could easily count bats at all sites because most animals were visible to the naked eye.

Monitoring winter activity

The number of hibernating bats was monitored across all seven roosts at Anseong and Hampyeong during winter of 2007–2008. Detailed winter activity was examined through tracking marked individuals. Winter activity was defined as inter-migration within a hibernaculum and switching between hibernacula during December and March, the hibernation period for most temperate-zone bat species (Lesiński 1986; Kokurewicz 2004; Boyles et al. 2006).

An individually coded ring was attached to the forearms of captured bats during pre-hibernation (October 2007). Anseong bats were banded with metal rings distinguishable through unique numbers, while Hampyeong bats were banded with plastic numbered rings (each hibernaculum was assigned a different ring color) (Fig. 1). Before attachment, plastic-ring edges were trimmed to minimize the potential for tissue damage. Bats were released into their roosts immediately after banding. Respectively, 131 and 21 bats were banded in Hampyeong and Anseong.

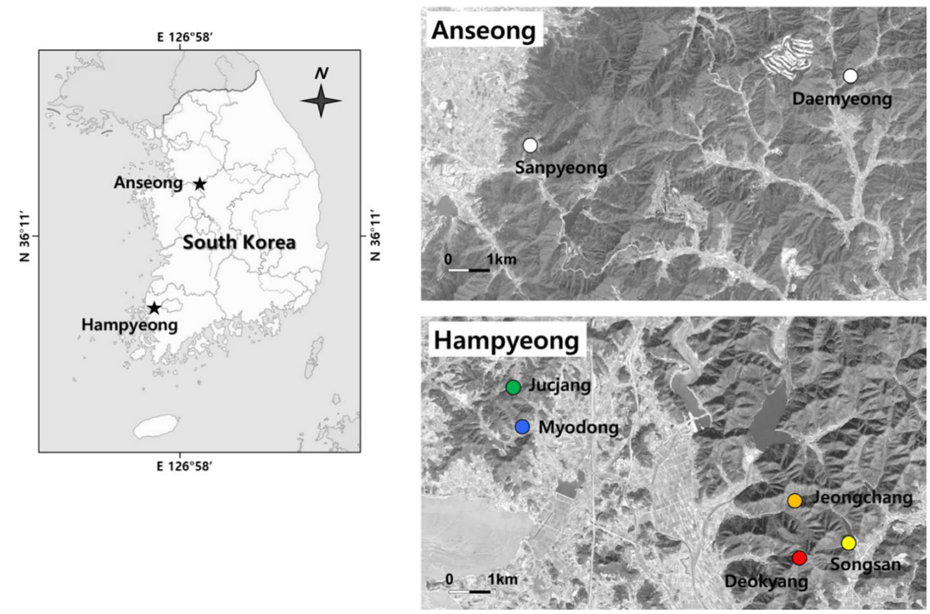

Fig. 1 Study sites at Anseong (2 sites) and Hampyeong (5 sites). Colored dots in the Hampyeong map indicate marking ring colors used for that site

Bat movements were tracked monthly through recording marked individuals in roosts.

Hibernating bats primarily use stored body fat for energy (John 2005). To determine mass loss across the hibernation period, torpid bats were weighed using a hand-held digital balance (0.1 g accuracy, HH-120, Ohaus), once early in hibernation (October–November 2007 in Anseong and December 2007 in Hampyeong), then again during late hibernation (March 2008). Measurements occurred within 1 min and were performed immediately below the place where the subject was sampled. After weighing, bats were returned to the same location. No bats woke because of disturbance. These described methods in accordance with recommended guidelines for monitoring European bat species (Jones and McLeish 2004).

Measuring temperature in hibernacula

Portable data loggers (EL-USB-2 Temp/RH, Lasca Electronics Ltd., England) were used to track hourly fluctuations in inner ambient temperature of hibernacula. Loggers were installed during October before hibernation began, in a part of the hibernaculum where many bats would be roosting. After hibernation, logged data were downloaded to a laptop computer for analysis. Daily external temperatures were obtained from the Meteorological Station in Mokpo (34° 49′ 1″ N, 126° 22′ 51″ E) and Cheonan (36° 45′ 43″ N, 127° 17′ 34″ E), approximately 30 km and 20 km from Anseong and Hampyeong, respectively.

Data analysis

Variation in the number of individuals per hibernaculum was evaluated using an index of fluctuation (Fi, range 0 to 1). A small Fi indicates a stable number of individuals between hibernacula, while a large Fi indicates instability and individuals moving between hibernacula.

Results

Bat winter activities during the hibernation period

We confirmed that some hibernating bats moved to other hibernacula. During the hibernation period (December 2007 to March 2008), more variation in bat number occurred at Hampyeong (index of fluctuation, Fi = 0.248–0.682) than at Anseong (Fi = 0.024–0.074). Among the five Hampyeong sites, we observed significant monthly changes in bat abundance, whereas the two sites in Anseong did not experience such changes. These data indicate that Hampyeong bats engaged in activity outside hibernacula more frequently than Anseong bats.

At Hampyeong, we confirmed bat movement both within and between hibernacula during the hibernation period. Of the 167 bats marked during pre-hibernation (October 2007), 97 bats were observed during the hibernation period. We found only four in the same hibernation site consistently, whereas the remaining animals were

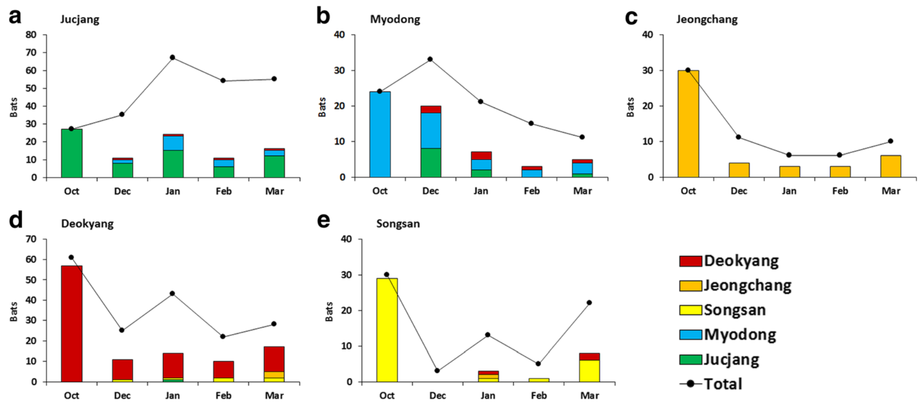

Fig. 2 a–e Monthly variation in total number (line graph) and marked individuals (bar graphs) of greater horseshoe bats hibernating in five hibernacula from Hampyeong. Bar colors correspond to marking ring colors at each hibernaculum during pre-hibernation (October 2007)

identified in two or more hibernation areas. Across four surveys, 19 bats (19.6%) moved once, 60 (61.9%) moved twice, and 14 (14.4%) moved three times (Fig. 2).

At Anseong, we did not confirm any between-hibernacula movement, although within-hibernaculum movement was evident. Compared with the hibernation period, bats moved into their roosts more often during January and February, when the ambient temperature of hibernacula interior decreased. Bat movement appeared to correlate with variation in hibernaculum ambient temperature, which in turn responded to temperature fluctuation outside.

Hampyeong bats were more likely to move between hibernacula of close proximity (Fig. 2). The similarity index splits bats into two groups based on site usage: the first included Duckyang, Jeongchang, and Songsan, while the second included Jukjang and Myodong. The locations in each groups were separated by approximately 1 km.

Ambient hibernacula temperatures

Average winter temperatures are − 7.3 to 11.7 °C in Anseong (central Korea, N 36° 55′ 13″, E 127° 16′ 11″) and − 7.3 to 11.7 °C and − 3.1 to 11.3 °C in Hampyeong (southern Korea, N 35° 06′ 40″, E 126° 29′ 48″) (Fig. 3 and Table 1). Anseong experienced 22 days during which the daily average temperature was > 5 °C, whereas Hampyeong experienced 50 days in early December and late March (Table 1). In addition, the two sites differed in the duration of below-freezing temperatures that would affect nearby reservoirs, with Anseong and Hampyeong experiencing 44 and 10 days of < 0 °C weather, respectively.

During the hibernation period, hibernacula in Anseong had relatively higher internal ambient temperatures (6.5–10.5 °C) than in Hampyeong (2.2–10.1 °C) (Fig. 4). Temperatures were more stable within the two hibernacula at Anseong than hibernacula at Hampyeong and appeared less influenced by external temperature variation. In contrast, internal temperatures of Hampyeong hibernacula varied considerably in response to external temperatures. Specifically, within Hampyeong, hibernacula of Myodong and Juckjang experienced similar temperature fluctuations, as did hibernacula of Jeongchang, Deokyang, and Songsan.

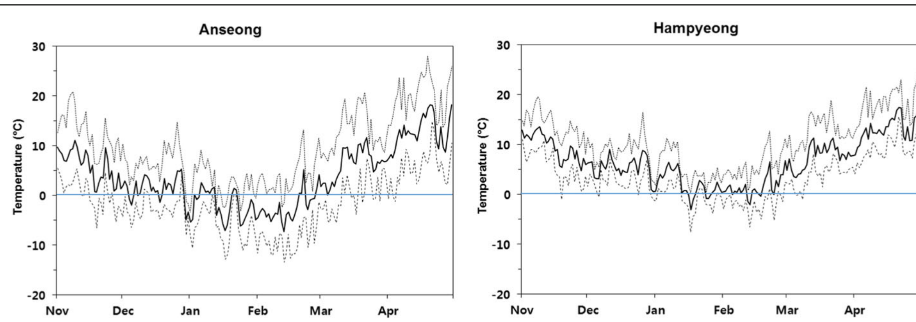

Fig. 3 External ambient temperature at Anseong and Hampyeong during winters of 2007–2008. The solid line indicates daily mean temperatures, while the upper and lower dashed lines indicate daily maximum and minimum temperatures, respectively. The horizontal line represents zero temperature

Table 1 Number of days in which daily temperatures was > 5 °C and < 0 °C in Anseong and Hampyeong during winter (December 2007 to March 2008)

	Anseong				Hampyeong			
	Avg. temp		Min. temp		Avg. temp		Min. temp	
	> 5 °C	< 0 °C	> 5 °C	< 0 °C	> 5 °C	< 0 °C	> 5 °C	< 0 °C
December	1	5	0	27	19	0	3	4
January	0	20	0	28	5	6	0	17
February	1	24	0	29	2	4	0	26
March	20	0	5	16	24	0	9	3
Total (days)	22	49	5	100	50	10	12	50

Variation of bat body mass during the hibernation period

Bat body mass decreased during hibernation in both test areas (Table 2). Hampyeong bat weights dropped from 22.16 g ($n = 115$) during early hibernation (December 19, 2017) to 17.96 g ($n = 111$) at the end of hibernation (March 27, 2008). Daily decrease was 0.043 g across 98 days. Anseong bat weights decreased from 24.72 g (October 28, 2007, $n = 45$) to 20.41 g (March 9, 2008, $n = 46$) at Sanpyeong, a daily reduction of 0.033 g over 132 days. At Daemyeong, weights dropped from 23.84 g (November 24, 2007, $n = 10$) to 19.77 g (March 9, 2008, $n = 12$), a daily decrease from 0.033 to 0.039 g.

Discussion

In this study, we observed clear evidence of bat activity during hibernation, despite the overall low insect abundance outside hibernacula and extremely cold temperatures. Previous studies have suggested that bats leave hibernacula in winter to feed (Ransome 1968; Avery 1985; Park et al. 2000; Geluso 2007) or drink (Speakman and Racey 1989; Speakman and Rowland 1999; Boyles et al. 2006; Geluso 2007; Turbill 2008). However, our results did not support the feeding hypothesis.

Regardless of mechanism, research describing bat activities during the hibernating period makes important contributions to a full understanding of hibernation (Boyles et al. 2006). Identifying the purpose of bat activity during hibernation will enhance our understanding of hibernation mechanisms and bat ecology, thus contributing to improved conservation and habitat management (Speakman and Racey 1989; Thomas and Geiser 1997; Park et al. 2000). Between-species variation in winter torpor behaviors is likely a response to differing physiologies and regional climates (Jonasson and Willis 2011). Therefore, ecological and physiological variation across species must be clarified first before we can develop a cohesive explanation of bat arousal and activity during the winter hibernating stage (Boyles et al. 2006; Geluso 2007).

Ambient temperature influences seasonal and daily activity patterns of many temperate bat species (Kunz 1982; Speakman and Thomas 2003). Ambient air temperature has a well-supported positive correlation with elevated winter activity in some species (Whitacker and Rissler 1992; Park et al. 2000; Geluso 2007; Turbill 2008). The reason for this relationship appears to be the temporary increase in insect activity under elevated temperatures, leading to more hunting opportunities for bats. Bats may need to

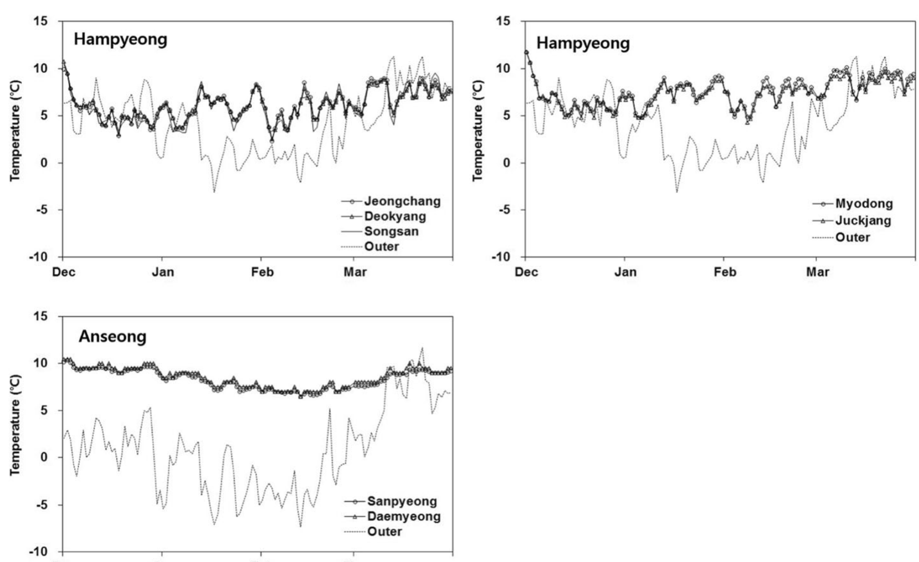

Fig. 4 Inner ambient temperatures of five hibernacula in Hampyeong and two hibernacula in Anseong during the hibernation period (December 2007 to March 2008)

Table 2 Body mass loss among greater horseshoe bats in Hampyeong and Anseong during the hibernation period. Data from all five hibernacula in Hampyeong were pooled for same measurement date, but data from two hibernacula in Anseong were separated for different measurement date

Location	Hampyeong (five hibernacula are pooled)		Anseong			
			Sanpyeong		Daemyeong	
Measurement date	Early (Dec 19, 2007)	Late (Mar 27, 2008)	Early (Oct 28, 2007)	Late (Mar 9, 2008)	Early (Nov 24, 2007)	Late (Mar 9, 2008)
No. bats	115	111	45	46	10	12
Body mass (g)	22.16 ± 2.21	17.96 ± 1.30	24.72 ± 2.20	20.41 ± 1.66	23.84 ± 2.14	19.77 ± 1.55
Days	98		132		105	
Body mass loss (g)	4.20		4.30		4.07	
Daily mass loss (g/day)	0.043		0.033		0.039	

supplement energy expenditure on hibernation with occasional arousal to feed and increase energy reserves, but such behavior is only profitable if energy intake from feeding is greater than energy consumed from activity (Avery 1985; Brigham 1987; Whitaker and Rissler 1992; Park et al. 1999).

Ambient temperature has a considerable effect on insect flight activity, with the minimum temperature thresholds averaging around 8–17.5 °C (Taylor 1963). Temperatures in both Hampyeong and Anseong were below these thresholds. Despite these low temperatures and thus the presumed lack of high insect activity, we observed variation in bat number and noted movement between hibernacula at Hampyeong, even during the coldest months. We note, however, that because we could not track bat activity daily, we cannot demonstrate a one-to-one correlation between outside temperature fluctuations and bat activity.

In this study, bat weights by the end of hibernation were lower than their weight during April to September (20–30 g, Kim SS unpublished data), when bats were active. Our findings are in line with previous reports demonstrating that hibernating bats decreased in weight by 17–20% after hibernation, suggesting that bats used energy reserves without replenishment during the hibernation period (Kunz et al. 1998; Kokurewicz 2004; Boyles et al. 2007). Additionally, we did not find new feces in hibernacula during winter. Together, these data indicate that *R. ferrumequinum* is totally dependent on fat stored during pre-hibernation (Humphries et al. 2002; Speakman and Thomas 2003; John 2005), and supplementary feeding was not the cause of their winter activity.

We did find some evidence for the hypothesis that bats moved in winter to obtain sufficient water (Speakman and Racey 1989; Thomas and Geiser 1997; Speakman and Thomas 2003). Water requirements decrease considerably during hibernation (less than 1/10th the needs during summer; O'Farrell et al. 1971), and even without drinking, bats can generate water through lipid oxidation (Neuweiler 2000). Nonetheless, air conditions in most hibernacula result in unavoidable water loss that cannot be compensated by such metabolic processes (Neuweiler 2000). Indeed, laboratory experiments have shown that a hibernating bat can survive 9–12 days in torpor without water (Speakman and Racey 1989), so longer hibernation periods may need to be interrupted for drinking sessions.

The five studied roosts in Hampyeong did not have internal water sources, but a reservoir was present within a 1-km radius outside. This reservoir was rarely frozen during winter because the region did not experience below-freezing temperatures. Bats at this location switched frequently between hibernacula. In contrast, outside drinking sources were unavailable at Anseong because winter temperatures were consistently < 0 °C, whereas unfrozen groundwater was present within the hibernacula. We did not observe between-hibernacula movement at this location. These results lead us to conclude that bats may be moving outside because of water requirements, as previously suggested (Speakman and Racey 1989; Whitaker and Rissler 1992; Boyles et al. 2006; Turbill, 2008). Studies on bats in hibernacula with standing water revealed that individuals will drink opportunistically from these sources, confirming the need for rehydrating during winter while implying that bats in hibernacula without readily available water will be forced to leave the roost (Whitaker and Rissler 1992; Boyles et al. 2006). To conclude, hibernating bats may become active outside depending on internal environment (presence or absence of standing water within roosts) or external climate environment (availability of unfrozen water sources).

In a thermally fluctuating winter environment, bats may change roosts to find a more favorable place for hibernation (Boyles et al. 2006). In such cases, a single roost may not sufficiently provide for thermoregulatory needs throughout winter, so bats may use multiple sites to compensate for a lack of environment stability (Boyles et al. 2006). However, our results did not support this thermoregulation hypothesis. Specifically, Hampyeong bats switched frequently between hibernacula of similar temperatures, while Anseong bats did not move between their hibernation sites of similar temperatures. Together, these observations indicate that bat movement was independent of hibernacula environment and therefore unlikely to be caused by thermoregulatory needs.

Conclusion

In this study, we confirmed that bat movement patterns differed significantly between regions, largely because of temperature and roost-environment variations. Neither region had external winter temperatures that favored bat feeding behavior. However, bats at Anseong have access to groundwater in their hibernacula when the external reservoir is frozen, whereas bats at Hampyeong can rely on an unfrozen external reservoir even without groundwater access. This slight temperature variation between the two regions and differences in hibernacula water access are the most plausible explanations for observed winter activity in *R. ferrumequinum*. In conclusion, our results provide insight into the hibernation strategies of bat populations in the temperate zone. Furthermore, this study highlights gaps in our understanding of bat winter activity, promoting new directions for future research.

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Availability of data and materials
The datasets during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Authors' contributions
SSK, YSC, and JCY designed the study. SSK and YSC equally participated in collecting and analyzing the data and writing the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate
Not applicable

Consent for publication
Not applicable

Competing interests
The authors declare that they have no competing interests.

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