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Research article

Effects of multiple ecological factors on the body mass of small rodents in a forest ecosystem

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The body mass of animals is directly or indirectly affected by multiple ecological factors. However, the effects of ecological factors on the body mass are controversial, and a comprehensive study dealing diverse ecological factors is rare. This study was performed to determine the effects of ecological factors on the body mass of small rodents in a natural deciduous forest located on Mt Gariwang, Pyeongchang and Jeongseon, South Korea from May 2019 to October 2020. We classified ecological factors into topographic, climatic, cover and demographic factors. Three forest-dwelling small rodent species, striped field mouse *Apodemus agrarius*, Korean field mouse *A. peninsulae* and red-backed vole *Myodes regulus*, were captured using the capture–mark–recapture method. The findings showed that the body mass of three rodent species was not regulated by topographic factors. In addition, a high ambient temperature resulted in a heavy body mass for *A. agrarius* and *A. peninsulae*, and the *A. agrarius* body mass was negatively affected by extreme rainfall. The body mass of each rodent species had a specific response to the cover factors: ground vegetation, understory vegetation or downed trees. The three species showed sexual dimorphism and two *Apodemus* species competed each other. This study reveals that ecological factors affecting body mass differ among species. Our findings contribute to enhancing the understanding of variation in the body mass of animals, particularly small rodents, in response to diverse ecological factors.

Keywords: *Apodemus agrarius*, *Apodemus peninsulae*, climate, cover, demography, *Myodes regulus*

Introduction

The body mass of wildlife is determined by the energetic cost–benefit relationship, and consequently wildlife shows altered behavior to optimize energy efficiency based on habitat conditions (Romanach et al. 2007). The potential cost is defined as the negative effects of predation risk, competition for resources, infection from disease or parasites, and extreme weather conditions on fitness, whereas the potential benefit refers to the positive effects of foraging on fitness (Alcock 2005, Krebs 2009). These



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elements of potential cost and benefit are influenced by habitat conditions. Therefore, the body mass of wildlife is directly or indirectly affected by habitat conditions, and closely mirrors habitat conditions (Martin 2019).

Habitat conditions are determined by various ecological factors, such as topographic (e.g. altitude, area, slope aspect and slope gradient), climatic (e.g. temperature and precipitation), cover (e.g. vegetation and downed trees) and anthropogenic factors (e.g. habitat loss and habitat fragmentation) (Gilliam 2007, Kearney et al. 2007, Lee et al. 2022b). These factors are closely linked, and complexly affect the demographic factors (e.g. population size, survival rate and reproductive rate) of wildlife (Lee et al. 2018, Martin 2019). Therefore, the ecological factors in various way determine the body mass of wildlife.

The climatic factors affect the body mass of animals by directly stimulating their thermogenesis requiring energy (cost), especially in cold conditions or by indirectly modulating their habitat conditions including the characteristics of the vegetation (Wang et al. 2006, Guralnick et al. 2020). The topographic factors modulate microclimatic conditions and soil conditions, resulting in differences in the composition and structure of vegetation as an essential resource (benefit) for wildlife (Pintado et al. 2001, Chun et al. 2020, Lee et al. 2020). Cover factors determine the availability of diverse food and shelter resources (benefit) for animals, which in turn control their body mass (Muñoz et al. 2009, Lee et al. 2019). The demographic factors cause differences in the body mass of individuals depending on sex, age structure and population size of conspecific and other sympatric species (Schulte-Hostedde 2008, Mason et al. 2014, Jarvis et al. 2017). In particular, population sizes of conspecific and other sympatric species modulate the extent of intra- and interspecific competition, respectively, resulting in variation in the body mass of individuals (Gurnell et al. 2004).

Rodents are the most diverse and abundant mammals constituting more than 40% of mammal species and inhabiting a broad geographic range (Honeycutt et al. 2008, Alhajeri et al. 2020). They serve as important components of the global food web in diverse ecosystems as consumers, prey and seed dispersers (Boggs et al. 2020, Salek et al. 2020). Moreover, demographic features of small rodents quickly respond to environmental changes (Lee et al. 2018).

The body mass of small rodents has been studied to explain the regulation of its change patterns by different ecological factors, such as topography (Medina et al. 2007, Wen et al. 2021), climate (Khokhlova et al. 2001, Alhajeri and Steppan 2016, Guralnick et al. 2020), cover (Banks and Dickman 2000, Muñoz et al. 2009, Alhajeri et al. 2020) and demography (Fasola and Canova 2000, Michaux et al. 2002). However, these studies have mostly considered only one type of ecological factors and the conclusions are somewhat controversial among them. Therefore, more comprehensive studies that investigate different ecological factors simultaneously are needed for a deeper understanding of small rodent body mass change patterns (Maestri et al. 2016). There is a lack of such comprehensive studies in particular areas, especially in

South Korea where most studies on the relationship between rodents and ecological factors have focused on rodent population size as an indicator (Kang et al. 2013, Son et al. 2021).

This study was performed to determine the effects of diverse ecological factors on the body mass of small rodents in a natural deciduous forest in South Korea. We evaluated the effects of four ecological factors: topography (altitude and slope gradient), climate (temperature and precipitation), cover (food and shelter resources) and demography (sex and intra- and interspecific competition) on the body mass of small rodents. We formulated four hypotheses: the body mass of small rodents decreases as the altitude gets higher because foraging efficiency declines at the high altitude characterized by low available resources and temperatures; a high temperature increases body mass of small rodents because of a positive effect of high temperature on their thermoregulatory mechanisms; the body mass of each rodent species is affected by different cover factors based on its microhabitat preference; ecologically similar species affect each other's body mass because of their niche overlap.

Material and methods

Study area and experimental design

This study was conducted on Mt Gariwang (37°27.5'–37°30.5'N, 128°30.5'–128°33.5'E), Pyeongchang and Jeongseon, South Korea from May 2019 to October 2020 (Fig. 1a and b). This mountain covers an area measuring approximately 40 km², and its altitude is 1561 m above sea level (a.s.l.). The annual mean temperature and annual precipitation during the study period were 11.17°C and 1052.15 mm, respectively. The vegetation of Mt Gariwang is comprised of temperate deciduous, coniferous and mixed forests (Chun et al. 2020).

A set of two 100 × 100 m (1 ha) study plots was randomly located at 900, 1100 and 1300 m a.s.l. in a natural deciduous forest to minimize anthropogenic factors, which were not evaluated in this study (Fig. 1c). The two study plots located in the same altitude were separated by more than 100 m to inhibit the migration of small rodents between the two plots (Lee and Rhim 2016). There were no individuals migrating between the study plots in this study. We set up a 7 × 7 grid (i.e. 49 trapping points per plot) with 15 m intervals in each of the six study plots.

Survey of topographic, climatic and cover factors

We measured the altitude (meters above sea level) and slope gradient as topographic factors at each trapping point using a portable GPSMAP and a laser measuring tool (Forestry Prom Nikon Vision Co., Ltd., Tokyo, Japan), respectively. The measured slope gradient was standardized using the following formula: standardized slope gradient = slope gradient/90 × 200% (Chai and Wang 2016).

The temperature during the study period was recorded at hourly intervals using three Hobo data loggers (Onset

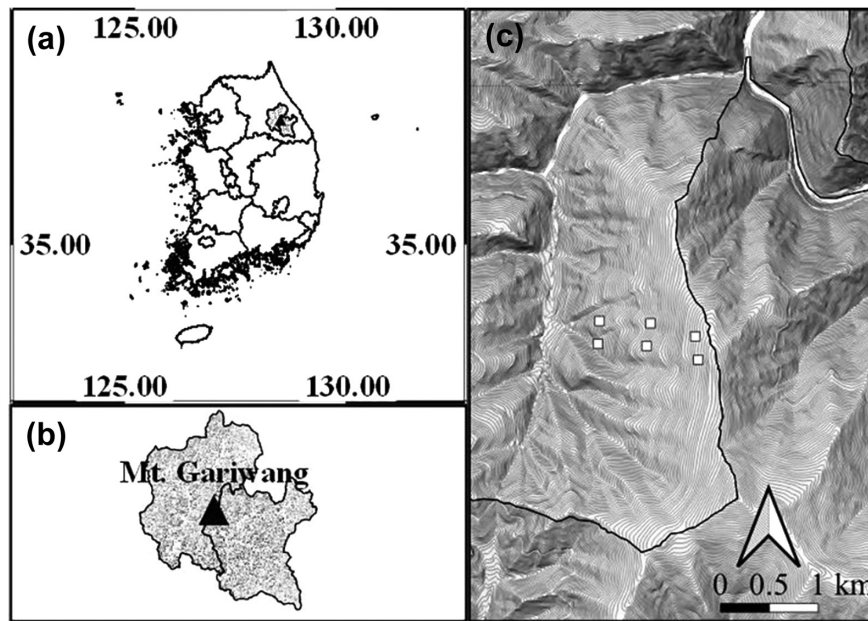


Figure 1. Location of the study area in a natural deciduous forest located on Mt Gariwang, Pyeongchang and Jeongseon, South Korea from May 2019 to October 2020. (a) Location of Pyeongchang and Jeongseon (grey color) in South Korea; (b) location of Mt Gariwang (black triangle) in Pyeongchang and Jeongseon; (c) location of six study plots (white box) in Mt Gariwang.

Computer Corporation, Massachusetts, USA) placed at 900, 1100 and 1300 m a.s.l. Precipitation data was collected from the Korea Meteorological Administration Weather Data Service. Temperature and precipitation were calculated as monthly mean temperature ($^{\circ}\text{C}$) and monthly total precipitation (mm), respectively.

Cover factors reflecting microhabitat conditions were measured from July to August in 2019 and 2020. We set up a circle with a 5.64 m radius centered on each trapping point and surveyed the following features: ground vegetation coverage (0–1 m height), understory vegetation coverage (1–2 m height), stone coverage (%), tree basal area ($\text{m}^2 \text{ha}^{-1}$), number of standing trees and downed trees (n ha^{-1}) and volume of downed trees ($\text{m}^3 \text{ha}^{-1}$). We categorized the values of vegetation coverage into the following four groups: 0 (coverage = 0%), 1 (1–33%), 2 (34–66%) and 3 (> 67%).

Capture of small rodents

Small rodents were captured using Sherman live traps ($7.62 \times 8.89 \times 22.86$ cm) placed at each of the trapping points from May to October in 2019 and 2020. We used the capture–mark–recapture method to identify captured individuals and estimate population sizes. The traps were baited with peanuts, activated during three consecutive nights in each month, and checked every morning. We marked each captured small rodent with an identification (ID) number together with toe clipping or ear punching. We recorded the capture place, ID number, species, sex, age (adult or juvenile), reproductive condition of each animal, and measured their body mass using a spring balance to nearest 0.1 g (Pesola AG, Baar, Switzerland). Thereafter, the captured individuals

were immediately released at the trapping point at which they were captured.

Estimation of small rodents' population size as a demographic factor

To determine the effects of intra- and interspecific competition on the body mass of small rodents, we estimated the population size of small rodents using the 'Rmark' package in R (Laake 2013, www.r-project.org). The Jolly–Seber model with POPAN parameterization was used to calculate the population size of each rodent species in each of the six plots in each year. Therefore, we made 12 models for the population estimation in total. These models included four parameters: ϕ (apparent survival), p (capture probability), $pent$ (entry probability), n (super population size). The global model was as follow: ϕ (species $\times$ time), p (speciestime), $pent$ (species $\times$ time), n (species). We selected the best models based on the Akaike information criterion with corrections for small samples (AICc) because Burnham and Anderson (2002) suggested to always use AICc than AIC regardless of the numbers of sample and estimated parameters. In the analysis of each rodent species, the population size of the conspecific was used as the variable for intraspecific competition, and the population sizes of the other species were utilized as the variable for interspecific competition.

Processing of body mass data

A total of 1492 body mass measurements plus the associated data from the total captures were collected during the study period. Seventeen body mass measurements of Siberian

chipmunk *Tamias sibiricus* were removed because the sample size was too small for analysis. We discarded 158 body mass measurements where one or more of the associated data items had not been recorded, as well as 123 body mass measurements of rodents that died in the trap. The high trap mortality in our study appeared to be due to unexpected extreme weather conditions, especially heavy rainfall. Because only adult data was used, the body mass measurements of 171 juveniles were also discarded, as were the data for 43 pregnant females with obvious pregnant condition, copulatory plug and enlarged nipple. In addition, to prevent surveyor error, we excluded 13 outliers locating beyond 1.5 times the interquartile range (IQR) using a boxplot of the entire data set (Benhadi-Marín 2018). Thus, a total of 967 body mass measurements plus associated data were used to determine the comprehensive effects of ecological factors on the body mass of small rodents.

Data analysis

Prior to all data analyses, a normality test for all the ecological factors was performed using the Shapiro–Wilk test. Basal area, numbers of standing trees and downed trees, and volume of downed trees were log-transformed to approximately comply with normality. Thereafter, a Spearman correlation analysis was conducted to remove the multicollinearity between variables belonging to each ecological factor category. We eliminated one variable of each pair (Spearman's coefficient > 0.7) depending on the ecological meaning or correlation with the dependent variables (i.e. the body mass of small rodents) (Carrilho et al. 2017). We discarded stone coverage correlated with ground vegetation ($r = -0.76$) by this process.

We conducted linear mixed models (LMMs) to evaluate the effects of topographic, climatic, cover and demographic factors on the body mass of small rodents at an individual level using the 'lme4' package in R (www.r-project.org, Bates et al. 2015). Each species was separately tested. The global models of the LMMs were as follows: body mass ~ altitude + standardized slope gradient + temperature + precipitation + ground vegetation + understory vegetation + number of standing trees + basal area + number of downed trees + volume of downed trees + sex + population size of each species. Random effects included trapping points. We used the 'dredge' function in the 'MuMIn' package to construct all candidate models (Barton 2018), and selected the model with the lowest AICc among the candidate models.

Results

We achieved 1492 captures of 793 individuals (striped field mouse, *Apodemus agrarius*: 243 captures of 137 individuals; Korean field mouse, *A. peninsulae*: 479 captures of 244 individuals; red-backed vole, *Myodes regulus*: 753 captures of 399 individuals; and *T. sibiricus*: 17 captures of 13 individuals) during 8820 trap-nights. The numbers of captured male and female were shown in the Supporting information. Because

525 body mass measurements were discarded during data processing, 147 *A. agrarius*, 343 *A. peninsulae* and 477 *M. regulus* body mass measurements were used as the dependent variable to explain the comprehensive effects of ecological factors on body mass.

Topographic effects on the body mass of small rodents

Slope gradient among the topographic factors was only included in the best model for *M. regulus* (Supporting information). However, it was not significant to the body mass of *M. regulus* ($\beta = 0.0313$, $SE = 0.0214$, $t = 1.464$, $p = 0.145$; Fig. 2). Therefore, we did not find any topographic effects on the body mass of small rodents.

Climatic effects on the body mass of small rodents

The best model for *M. regulus* did not include any climatic factors (Supporting information). Temperature appeared to positively affect the body mass of two *Apodemus* species (*A. agrarius*: $\beta = 0.4449$, $SE = 0.1688$, $t = 2.635$, $p = 0.009$; *A. peninsulae*: $\beta = 0.2994$, $SE = 0.0941$, $t = 3.182$, $p = 0.002$; Fig. 3a). However, a high precipitation decreased the body mass of *A. agrarius* ($\beta = -0.0104$, $SE = 0.0047$, $t = -2.209$, $p = 0.029$; Fig. 3b).

Cover effects on the body mass of small rodents

The best model for *A. agrarius* included the number of downed trees, whereas the best *A. peninsulae* model consisted of the ground vegetation coverage and the understory vegetation coverage (Supporting information). The best model

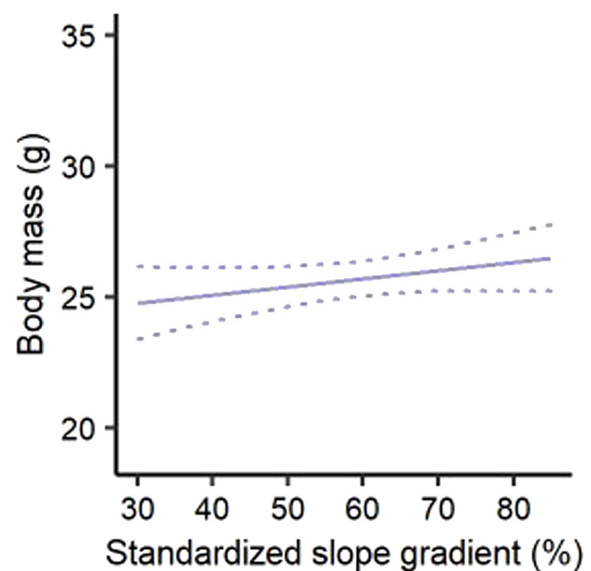


Figure 2. The effects of topographic factors on the body mass of red-backed vole *Myodes regulus* in a natural deciduous forest located on Mt Gariwang, Pyeongchang and Jeongseon, South Korea from May 2019 to October 2020, determined using the best model selected from the linear mixed models.

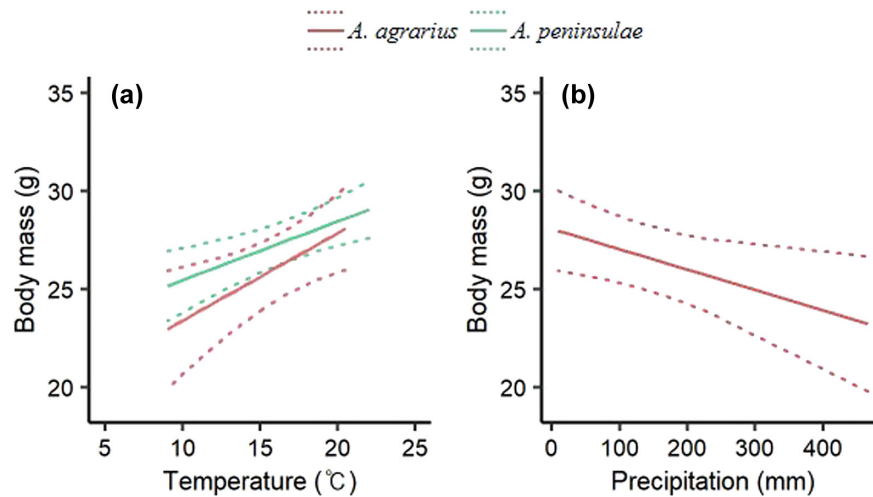


Figure 3. The effects of climatic factors on the body mass of two small rodent species, (a), (b) striped field mouse *Apodemus agrarius*, (a) Korean field mouse *A. peninsulae* in a natural deciduous forest located on Mt Gariwang, Pyeongchang and Jeongseon, South Korea from May 2019 to October 2020, determined using the best models selected from the linear models.

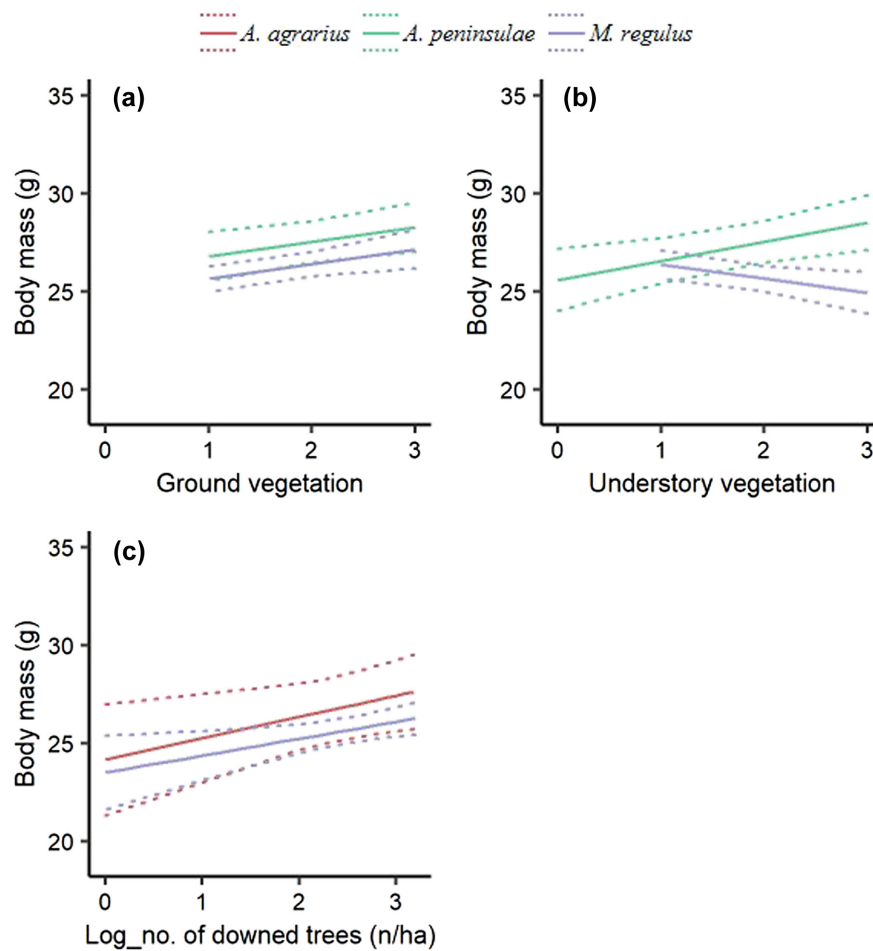


Figure 4. The effects of cover factors on the body mass of three small rodent species, (c) striped field mouse *Apodemus agrarius*, (a), (b) Korean field mouse *A. peninsulae* and (a)–(c) red-backed vole *Myodes regulus* in a natural deciduous forest located on Mt Gariwang, Pyeongchang and Jeongseon, South Korea from May 2019 to October 2020, determined using the best models selected from the linear mixed models.

for *M. regulus* included the ground vegetation coverage, the understory vegetation coverage and the number of downed trees. The ground vegetation had positive effects on the body mass of *A. peninsulae* ($\beta=0.7329$, $SE=0.3303$, $t=2.219$, $p=0.028$; Fig. 4a) and *M. regulus* ($\beta=0.7581$, $SE=0.2827$, $t=2.682$, $p=0.008$). The understory vegetation increased the body mass of *A. peninsulae* ($\beta=0.9712$, $SE=0.3647$, $t=2.663$, $p=0.008$; Fig. 4b), whereas individuals of *M. regulus* appeared to be lighter in microhabitats with dense understory vegetation ($\beta=-0.7338$, $SE=0.3071$, $t=-2.390$, $p=0.018$). The *A. agrarius* ($\beta=1.0915$, $SE=0.5201$, $t=2.099$, $p=0.038$; Fig. 4c) and *M. regulus* ($\beta=0.8658$, $SE=0.3628$, $t=2.387$, $p=0.018$) populations were heavier in microhabitats with many downed trees.

Demographic effects on the body mass of small rodents

The best models of three rodent species included the population size of *A. agrarius* and sex, and the population size of *M. regulus* was additionally subsumed under the *M. regulus* model (Supporting information). The population size of *A. agrarius*

appeared to positively affect the body mass of *A. agrarius* ($\beta=0.0487$, $SE=0.0233$, $t=2.094$, $p=0.039$; Fig. 5a) and *M. regulus* ($\beta=0.0202$, $SE=0.0089$, $t=2.267$, $p=0.025$), whereas individuals of *A. peninsulae* were lighter in microhabitats with highly inhabited by the *A. agrarius* population ($\beta=-0.0304$, $SE=0.0132$, $t=-2.308$, $p=0.022$). The body mass of *M. regulus* appeared to be heavier as the population size of conspecific individuals increased ($\beta=0.0159$, $SE=0.0055$, $t=2.878$, $p=0.004$; Fig. 5b). Males were heavier than females in the population of all three rodent species (*A. agrarius*: $\beta=5.3363$, $SE=0.9410$, $t=5.671$, $p<0.001$; *A. peninsulae*: $\beta=1.6016$, $SE=0.5947$, $t=2.693$, $p=0.007$; *M. regulus*: $\beta=1.1833$, $SE=0.3734$, $t=3.169$, $p=0.002$; Fig. 5c).

Discussion

In this study, we assessed the effects of four ecological factors: topography, climate, cover and demography on the body mass of three rodent species. First, we did not find any effects of topographic factors on the body mass of three species.

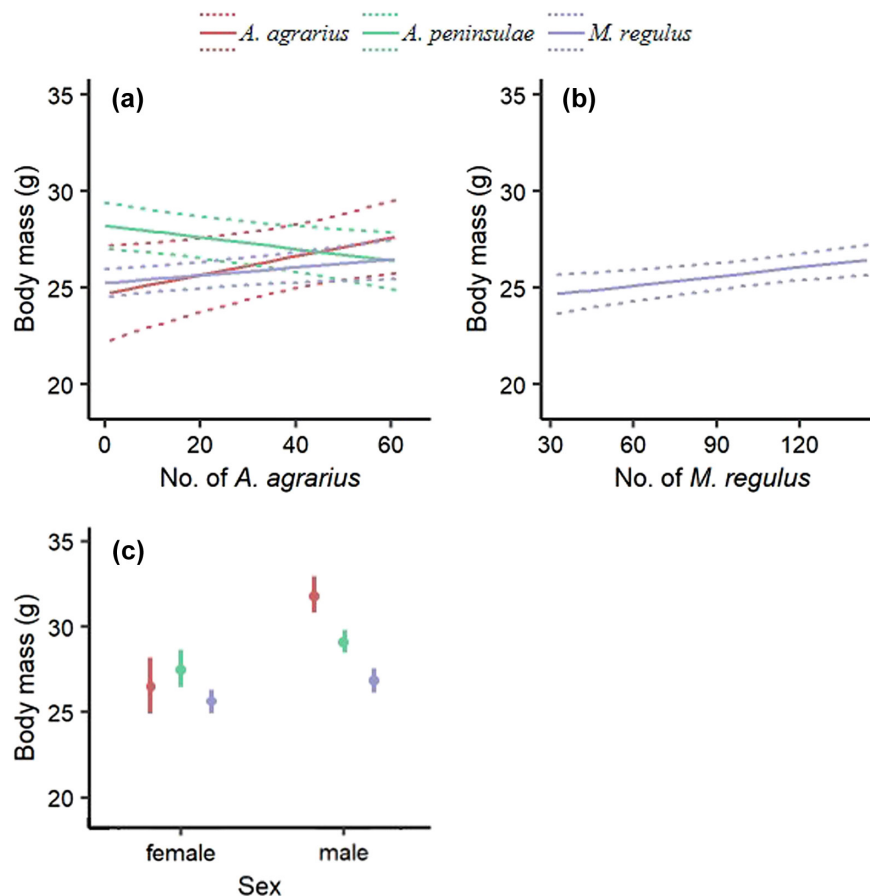


Figure 5. The effects of demographic factors on the body mass of three small rodent species, (a), (c) striped field mouse *Apodemus agrarius*, (a), (c) Korean field mouse *A. peninsulae* and (a)–(c) red-backed vole *Myodes regulus* in a natural deciduous forest located on Mt Gariwang, Pyeongchang and Jeongseon, South Korea from May 2019 to October 2020, determined using the best models selected from the linear mixed models.

Second, regarding the climatic factors, a high temperature resulted in a heavy body mass for *A. agrarius* and *A. peninsulæ*, and the *A. agrarius* population was negatively affected by high precipitation. Third, all three rodent species showed particular responses to different cover factors, such as ground vegetation, understory vegetation or downed trees. Lastly, we found sexual dimorphism and the negative effect of the *A. agrarius* population on the body mass of *A. peninsulæ*.

We captured three forest-dwelling rodent species, *A. agrarius*, *A. peninsulæ* and *M. regulus*. These species mostly inhabit diverse forests within mountain systems in South Korea (Jo et al. 2018). In the previous studies, they were observed at a wide range of altitude in which is covered by forests (Lee et al. 2008, 2022a, Kang et al. 2013). Two *Apodemus* species were reported to adopt daily torpor by reducing their metabolisms to save energy, under conditions with low temperature and food shortage (Masaki et al. 2005, Yoon and Han 2006), and thus are likely to be more sensitive to the temperature more than *M. regulus*. The three rodent species mostly utilize grass, shrub and downed trees as food and shelter resources, and each preference appears to be variable in response to surrounding environments (Rhim and Lee 2001, Lee et al. 2018, Son et al. 2021).

Our results showed that the ecological factors affecting the body mass of small rodents varied among three species. It appears to be due to the distinct preferences of each species. Each rodent species has a distinct habitat preference considering requirements such as food, shelter and nesting (Horvath et al. 2001). This distinct preference is a strategy to reduce competition with other species via resource-niche partitioning (Finke and Snyder 2008). The ecological factors influence their habitat preferences through modulating the habitat requirements.

In this study, although we expected that the body mass of small rodents decreases as the altitude gets higher, we did not observe any topographic effects on the body mass of three rodent species. In a mountainous system, altitude causes local-scale differences in the microclimate (e.g. temperature and humidity) and soil conditions (e.g. soil composition and soil texture) (Jucker et al. 2018). Therefore, the abundance and distribution of vegetation are affected by variations in altitude, as temperature, water availability and soil nutrients are key for plant growth and survival factors (Krebs 2009, Al Balasmeh and Karmaker 2020). In particular, understory vegetation grows abundantly in low altitude because of the high temperature and superior soil nutrients in these areas (Coll et al. 2011, Gutiérrez-Girón et al. 2015, Lee et al. 2022a). However, it is difficult for ground vegetation to grow and survive in areas with dense understory vegetation because it is deprived of resources such as sunlight and soil nutrients by the understory vegetation (Pierce et al. 2019). Consequently, ground vegetation well establishes within an area with sparse understory vegetation (Lee et al. 2022a). In this study, only *A. peninsulæ* among three rodent species preferred both ground and understory vegetations, whereas *A. agrarius* and *M. regulus* positively correlated with downed trees. Therefore, it is likely that *A. peninsulæ* used ground

vegetation or understory vegetation, as alternative resources, within microhabitats with sparse understory vegetation or ground vegetation, respectively, and the populations of *A. agrarius* and *M. regulus* utilized downed trees regardless of altitude. These resource preferences appeared to offset the topographic effects on the body mass of small rodents in this study.

In the present study, we found that the body mass of *A. agrarius* and *A. peninsulæ* populations increased with an increase in temperature. These findings may reflect the positive influence of a high temperature on the thermogenesis of these species and their access to resources. Because animals must maintain homeostasis, they show higher thermoregulatory metabolism under cold compared to warm conditions (Rodríguez-Serrano and Bozinovic 2009). This finding corresponds to previous studies on variations in the body mass of small rodents related with temperature (Li and Wang 2005, Zhu et al. 2012). Furthermore, temperature are critical factors that regulate the growth and survival of plants providing food and cover resources to rodent species, especially within temperate and cold zones (Chang et al. 2014, Tang et al. 2017). In contrast to the temperature effects, precipitation appeared to have a negative effect on the body mass of individuals in the *A. agrarius* population. Previous studies demonstrated that rain was a limiting factor for the body mass of small rodents (Guralnick et al. 2020), and it impact differed based on rodent species (Brouard et al. 2020). During the study, the longest period of heavy rainfall days in South Korea since 1973 was recorded (54 days: 25 June–16 August 2020) (Korea Meteorological Administration 2021). This extreme weather condition may have negatively affected the foraging efficiency of this rodent population, potentially resulting in a negative effect on their body mass (Buchholz et al. 2019).

In the present study, the body mass of the small rodents appeared to be affected by ground vegetation, understory vegetation or downed trees, depending on the species. These findings may be because vegetation and downed trees supply food resources, such as soft leaves, stems, berries, lichens and invertebrates, as well as shelter (Kang et al. 2013, Earl et al. 2016, Jo et al. 2018). In addition, previous studies reported that food restriction decreased the body mass of small rodents (Zhu et al. 2013), food types relatively affected food intake and body mass depending on rodent species (Lobo and Millar 2011), and high predation risk restricted foraging activity of small rodents, resulting in lost body mass (Monarca et al. 2015). Furthermore, during our field trip, we observed some of the small rodents hiding under the vegetation and downed trees. It is likely that small rodent populations profit from a microhabitat with dense vegetation and many downed trees due to increased foraging efficiency (benefit) and decreased predation risk (cost), thus, these animals would be expected to have a heavy body mass in microhabitats with these cover features. However, the body mass of the *M. regulus* population decreased as understory vegetation was more abundant. *M. regulus* appeared to reduce an encounter with *A. peninsulæ*, to minimize a competition and save on energy cost (Lee et al. 2022a).

Our findings showed that the male small rodents were heavier than the females, and coincided with previous findings on *A. agrarius* (Balčiauskienė 2007) and other species (Boonstra et al. 1993, Ueda and Takatsuki 2005). It appears to be due to sexual dimorphism defined as differences in body composition between males and females (Schulte-Hostedde 2008). In general, male mammals have heavier muscle mass than females, especially rodents, because males require a physical advantage in intra-sexual competition for mates (Schulte-Hostedde et al. 2001). In the present study, except for the negative effect of *A. agrarius* population size on the body mass of *A. peninsulae*, we did not observe any evidence of competition. It appears to be caused by niche partitioning among sympatric species. Intra- or interspecific competition occurs for the acquisition of limited and overlapped resources between the same or different species (Namukonde et al. 2018). To avoid competition, rodents utilize different resources by niche partitioning (Finke and Snyder 2008). On the contrary, except for the *A. peninsulae* population, the body mass of each rodent species increased as the population size of the target species increased. Furthermore, the body mass of *M. regulus* increased as the population size of *A. agrarius* increased, even though both species used the resources provided by downed trees. Thus, our findings suggest that the sites we studied had a carrying capacity sufficient to adequately support all three rodent species. Our target habitats were located in a 50-year-old natural deciduous forest with minimal human disturbance and thus are likely to support suitable natural condition satisfying the habitat requirements of the target species. However, the body mass of the *A. peninsulae* population was negatively influenced by the population size of *A. agrarius*. This may be because these two species belong to the genus *Apodemus*, and thus their niche breadths overlap with each other more than with the niche breadth of *M. regulus*. In addition, Lee et al. (2018) reported that habitat use by *A. peninsulae* is restricted by an *A. agrarius* population.

In conclusion, we found that the body mass of each of three small rodent species was influenced by different ecological factors. The body mass of three rodent species was not affected by topographic factors, most likely due to alternative resources that they can use, regardless of altitude. High temperatures potentially lead to vigorous development of vegetation and low thermogenesis cost for rodents and thus may have resulted in the heavy body mass recorded for the *A. agrarius* and *A. peninsulae* population. However, the precipitation findings suggest that extreme rainfall suppresses the foraging efficiency of rodents, and thus may have caused the body mass loss recorded for *A. agrarius*. The three rodent species showed responses to particular cover factors, suggesting that they derived their benefits of food and shelter resources from different factors. We observed the negative effect of *A. agrarius* on the body mass of *A. peninsulae*, and this phenomenon may be due to niche overlap between two *Apodemus* species. Our findings contribute to a deeper understanding of the diverse ecological factors that influence the variation in body mass of animals, especially forest-dwelling small rodents. However, ours was a short-term study, and did not

consider other potential effects on small rodent body mass, such as those of anthropogenic factors. Furthermore, the body mass would not totally reflect animals' body conditions because each animal have different body water contents. Therefore, we propose that a long-term monitoring study, that include potential factors not considered in the present study, mitigate the high trap mortality by avoiding extreme weather conditions as much as possible, and consider other indicators of body conditions such as body length, is needed to improve the ecological knowledge about body condition change patterns in small rodents in response to a range of ecological factors.

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Conflict of interest – No potential conflict of interest was reported by the authors.

Permits – The experimental protocols for the treatment and care of animals were reviewed and approved under the guidelines of the local ethics committee (Institutional Animal Care and Use Committee, Chung-Ang University; approval number: CAU 2019-00028).

Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1zcrjdfwj> (Lee et al. 2022c).

Supporting information

The Supporting information associated with this article is available with the online version.

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