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Research article

Adaptive response of Siberian roe deer *Capreolus pygargus* to climate and altitude in the temperate forests of South Korea

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Understanding climatic effect on wildlife is essential to prediction and management of climate change's impact on the ecosystem. The climatic effect can interact with other environmental factors. This study was aimed to determine effects of climate and altitude on Siberian roe deer *Capreolus pygargus* activity in temperate forests of South Korea. We conducted camera trapping to investigate roe deer's activity level from spring to fall. Logistic regressions were used to determine effects of diel period, temperature, rain, and altitude on the activity level. A negative relationship was noted between temperature and the activity level due to thermoregulatory costs. Roe deer activity exhibited nocturnal and crepuscular patterns during summer and the other seasons, respectively, possibly due to heat stress in summer. In addition, the effect of temperature differed between high- and low-altitude areas. In low-altitude areas, temperature affected negatively the activity level throughout the study period. Conversely, in high-altitude areas, temperature affected activity level only in summer and early fall. Lower temperatures in higher altitudes favoured roe deer activity, resulting in roe deer's preference towards higher altitude areas. However, roe deer's movement toward lower altitudes was observed in summer. Reduced heat stress by changing activity pattern allowed them to access lower altitude areas with greater resource availability during summer. This study revealed how roe deer activity varied across seasons and altitudes, considering the interactions among weather, microclimate and resource availability. It provides insight into how montane species adapt to various climatic conditions, and this could have important implications for wildlife management and conservation efforts.

Keywords: behaviour, Cervidae, elevation, heat stress, microclimate, thermoperiod

Introduction

Climate change is a critical global issue that threatens many ecosystems. To predict and manage the impact of climate change on the ecosystem, several ecologists have investigated the complex mechanism by which climate affects animals' ecology (Davis et al. 2016, Weiskopf et al. 2019, Yusefi et al. 2021). On a broad scale, climate plays a key



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role in determining the distribution and migration of species (Brinkman et al. 2005, Levinsky et al. 2007, Jiang et al. 2020, Benjamin et al. 2022). On a smaller scale, weather and microclimate affect the physiology and behaviour of species (Muñoz-Delgado et al. 2004, Signer et al. 2011). In addition, climatic effects interact with other environmental factors, including habitat type, resource availability, interspecific interaction and community structure (Igota et al. 2004, Smolko et al. 2018).

An animal's activity reflects its ecological tactic for their survival and fitness. Their responses to numerous environmental factors can be observed in the activity pattern. Regarding Cervidae, their activity follows a circadian pattern that is affected by the daily photoperiod and thermoperiod (Jeppesen 1989, Jasińska et al. 2021). Their behavioural rhythm displays peaks at dawn and dusk, and the crepuscular pattern, thus, reflects seasonal changes in the timing of sunrise and sunset (Pagon et al. 2013, Zhou et al. 2022). In addition, deer consider ambient temperature in their activity to avoid unfavourable weather and maintain their body temperature. The behavioral thermoregulation encompasses both diel activity pattern and microhabitat selection. Responding daily temperature fluctuations, the deer can adjust their daily routine. Such thermoperiodic effects on deer activity vary across seasons and habitats (Schweiger and Frey 2021). As for seasonal variations, cold winter nights potentially restrain deer's nocturnal activity, and conversely, hot summer day potentially reduce their diurnal activity (Berger et al. 2002, Ikeda et al. 2015, Ikeda et al. 2016). In terms of habitat-dependent variations, roe deer in Europe exhibit distinct seasonal activity patterns depending on latitude. In southern Europe, the cold weather during winter reduces nocturnal activity of European roe deer *Capreolus capreolus* (Pagon et al. 2013). In contrast, the harsh cold weather during northern Europe's winters decreased roe deer activity throughout the entire day (Jeppesen 1989). Further, microclimate potentially influences roe deer activity, especially in relation to altitude. Since microclimate, including temperature and wind, can vary along altitudinal gradients, roe deer shift their habitat depending on altitude and season (Igota et al. 2004, Carvalho et al. 2008, Bojarska et al. 2020).

This study aimed to 1) examine the seasonal and altitudinal variations in roe deer activity from spring to fall and 2) determine how animals adapt to various climatic conditions within their habitat. We posed the following two hypotheses regarding season and altitude, as we anticipated. First, roe deer activity patterns would reflect seasonal variations in the thermoperiod. Second, roe deer activity would be potentially affected by altitudinal variations in the microclimate. This study's findings will augment current understanding regarding roe deer's adaptive strategies to the climate in montane habitats.

Material and methods

Study area

The study area was located in Mt Gariwang, Pyeongchang, South Korea (37°27'38"–37°30'35"N;

128°28'30"–128°33'56"E), which was 550–1500 m a.s.l. and constituted 3500 ha of temperate broadleaf mixed forest. The region's annual mean temperature was 7.04°C (–27.40 to 29.19°C), and the annual precipitation was 1668 mm. The altitudinal variation in temperature were observed in the study area (Lee et al. 2023), and the annual mean temperature at altitudes of 800, 1000 and 1200 m a.s.l. were recorded as 8.44°C (–23.84 to 29.19°C), 7.13°C (–25.44 to 27.36°C) and 5.57°C (–27.40 to 25.77°C), respectively. The study area comprised a temperate deciduous forest, dominated by Mongolian oak *Quercus mongolica*, and Japanese larch *Larix kaempferi* plantations. Two deer species exist in Mt Gariwang (Son et al. 2017): Siberian roe deer *Capreolus pygargus* and water deer *Hydropotes inermis*. The roe deer population was distributed across Mt Gariwang. A small water deer population inhabited the low-altitude (< 500–700 m a.s.l.) edge of the mountain. The yellow-throated marten *Martes flavigula* occasionally hunted fawns; however, this opportunistic predator's population density was low in the study area (no. of capture during 5910 trap-days in this study = 5). Public access to the entire area of Mt Gariwang was restricted, only allowing entry for foresters and researchers.

Camera trapping

The camera trapping method was used to observe temporal variations in roe deer capture (sampling days: September–October 2021 and April–August 2022). In order to mitigate temporal variation in population density, the study site was strategically located on a slope surrounded by steep valleys and hillside. Within the study site, a 5 × 6 grid design (interval = 600 m) was established, and one trail camera (Spec Ops Elite HP4; Browning Co., USA) was deployed corresponding to each cell of the grid. As grid system in the study area was sufficiently intensive, we assumed that it prevents sampling bias and reduce the variability in results. To increase the capture rate, a trail camera was placed on the ridge or animal trail, above 50–70 cm from the ground. The trail camera was set to record a 5 s video at each activation, with a 1 s triggering interval between activations. During video analysis, consecutive events within 30 min after the previous event were eliminated to exclusively use independent records. The study period was divided into five seasons, and further analyses were performed for each season: spring (15 April–15 May, 960 trap-days, n = 180), early summer (16 May–30 June, 1380 trap-days, n = 287), summer (1 July–31 August, 1860 trap-days, n = 515), early fall (September, 900 trap-days, n = 338) and fall (October, 810 trap-days, n = 123).

Data collection

To determine the study area's temperature, predicted temperature values were modelled at a reference-point altitude of 1000 m a.s.l., and used as a 'temperature' variable (*temp*). To construct the temperature model, we used reference-point temperature data from previous study (Lee et al. 2023) and weather data, including data on temperature and

relative humidity, from a certain weather station from April to October in 2019–2021. The weather station was located 560 m a.s.l., approximately 8 km away from the study area. The reference-point temperature was recorded with a 1 h interval using a weather data logger (HOBO U23 Pro v2; Onset computer Corp., USA). The temperature model explained well the relationship between the reference-point temperature and weather data from the weather station (Supporting information). Thereafter, predicted reference-point temperature values were calculated using the temperature model and weather data from the weather station during the study period.

A 'rainy day' variable (*rainy*) was established based on precipitation data from the weather station; it determined whether precipitation of sampling day was 0 mm or not. To explain altitudinal variations in temperature, an 'altitude' variable (*alt*) was used. The camera-plot altitudes were categorised into four classes: 600 (600–800 m a.s.l., $n=3$), 800 (800–1000 m a.s.l., $n=10$), 1000 (1000–1200 m a.s.l., $n=11$) and 1200 (1200–1400 m a.s.l., $n=6$). As we could not ascertain a linear relationship between altitude and roe deer activity, we integrated a categorical variable for altitude. The diel period (*diel*) was divided into dawn, day, dusk and night. Dawn and dusk were designated as the time within 2 h before and after sunrise and sunset, respectively.

Effects of climate and altitude on roe deer activity

In this study, only altitude was considered for the spatial variation in roe deer activity, since altitude was expected to make a spatial variation in temperature. Roe deer's activity level was analysed using weighted logistic regression and expressed as the observed probability per 2 h in each altitude class. Subsequently, sampling effort regarding altitude was accounted for by assigning a weight, the total number of plots / the number of plots at the altitude. A modelling procedure was conducted in each season to prevent seasonal variations in roe deer's population density. This facilitated the determination of the factors limiting roe deer activity in each season, rather than causing seasonal variations in their activity level. In each modeling procedure, a full model included the following explanatory variables and interaction terms between temperature and other factors: *temp*, *diel*, *alt*, *rainy*, *temp* $\times$ *diel*, *temp* $\times$ *alt* and *temp* $\times$ *rainy*. After constructing models using all possible combinations of variables from the full model, we selected candidate ($\Delta AIC_c < 2$) and the best-fit model based on the corrected Akaike information criterion (AIC_c). Post-hoc Tukey tests were performed to analyse the *diel* and *alt* variables in the top model. In addition, the effects of temperature were compared among the various diel periods and altitudes by estimating the trends' marginal means (Lenth et al. 2022). All statistical analyses were conducted using R software (ver. 4.2.2, www.r-project.org).

Results

The effects of climate and altitude on roe deer activity in each season were modelled (Table 1; Fig. 1–5). For spring

Table 1. Top models explaining the observed probability of Siberian roe deer *Capreolus pygargus* in Mt Gariwang, Pyeongchang, South Korea.

Predictors	Spring			Summer			Early fall			Fall		
	Log-odds (95% CI)	p		Log-odds (95% CI)	p		Log-odds (95% CI)	p		Log-odds (95% CI)	p	
(Intercept)	-2.45 (-2.91 to -2.02)	< 0.001		-2.84 (-4.53 to -1.22)	< 0.001		-5.38 (-8.45 to -2.36)	< 0.01		-2.47 (-2.95 to -2.02)	< 0.001	
diel (day)	-1.10 (-1.70 to -0.50)	< 0.001		0.86 (0.14–1.58)	0.02		3.88 (1.18–6.60)	< 0.01		0.37 (-0.14 to 0.89)	0.15	
diel (dusk)	0.48 (-0.19 to 1.14)	0.16		0.80 (-0.07 to 1.67)	0.07		9.02 (6.12–11.99)	0.02		-0.13 (-0.73 to 0.46)	0.67	
diel (night)	-0.47 (-0.93 to 0.00)	0.05		-0.94 (-1.54 to -0.34)	< 0.01		3.58 (1.04–6.12)	0.80		-1.60 (-2.16 to -1.05)	< 0.001	
temp	-0.09 (-0.16 to -0.02)	0.01		-0.08 (-0.12 to -0.04)	< 0.001		0.14 (-0.09 to 0.36)	0.32		-0.11 (-0.16 to -0.05)	< 0.001	
rainy	-0.12 (-0.33 to 0.07)	0.23		1.07 (0.49–1.64)	< 0.001		-0.35 (-0.58 to -0.12)	< 0.01		-1.12 (-1.94 to -0.35)	< 0.01	
alt (800)	0.82 (0.22–1.41)	< 0.01		1.35 (-2.24 to -0.49)	< 0.01		1.77 (-1.68 to 3.95)	0.42		-2.27 (-3.55 to -1.16)	< 0.001	
alt (1000)	1.09 (0.58–1.59)	< 0.001		-0.20 (-0.82 to 0.41)	0.52		3.77 (0.87–6.63)	0.01		2.09 (1.56–2.62)	< 0.001	
alt (1200)	1.33 (0.89–1.79)	< 0.001		-0.91 (-1.49 to -0.34)	< 0.01		3.62 (0.82–6.38)	0.01		1.14 (0.64–1.65)	< 0.001	
temp:diel (day)	0.07 (-0.00 to 0.15)	0.06		-0.11 (-0.16 to -0.05)	< 0.001		-0.36 (-0.56 to -0.17)	< 0.001		-0.07 (-0.12 to 0.02)	< 0.01	
temp:diel (dusk)	0.00 (-0.08 to 0.09)	0.91		-0.06 (-0.12 to -0.00)	0.04		0.10 (-0.19 to 0.40)	0.04		0.05 (-0.10 to 0.11)	0.08	
temp:diel (night)	0.07 (-0.01 to 0.14)	0.09		0.03 (-0.02 to 0.08)	0.20		0.31 (-0.05 to 0.67)	0.49		0.09 (0.04 to 0.15)	< 0.001	
temp:alt (800)	-0.02 (-0.09 to 0.05)	0.57		0.10 (0.04–0.16)	< 0.01		0.12 (-0.08 to 0.32)	0.25		0.27 (0.19–0.37)	< 0.001	
temp:alt (1000)	0.09 (0.04–0.15)	< 0.01		0.13 (0.09–0.17)	< 0.001		-0.06 (-0.26 to 0.15)	0.55		0.03 (-0.03 to 0.08)	0.36	
temp:alt (1200)	0.03 (-0.03 to 0.08)	0.33		0.15 (0.11–0.19)	< 0.001		-0.08 (-0.28 to 0.12)	0.42		0.07 (0.02–0.12)	0.01	
rainy:temp				-0.09 (-0.13 to -0.05)	< 0.001					0.08 (0.01–0.14)	0.02	

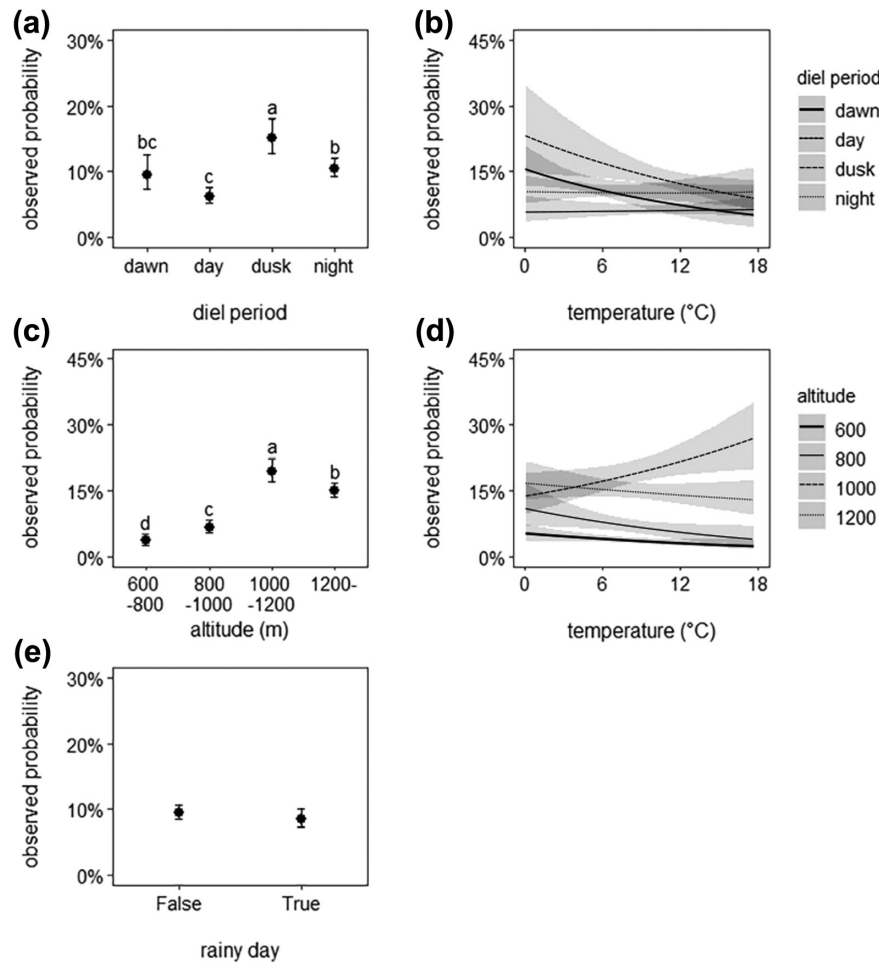


Figure 1. Effects of (a) diel period, (b) interaction between diel period and temperature, (c) altitude, (d) interaction between altitude and temperature and (e) rainy day on the observed probability of Siberian roe deer *Capreolus pygargus* in Mt Gariwang, Pyeongchang, South Korea during spring (15 April–15 May) based on logistic regression.

(χ^2 test for goodness-of-fit: deviance = -443.56, $p < 0.001$) and early-fall (deviance = -875.42, $p < 0.001$) analyses, the top model included the *temp*, *diel*, *alt*, *rainy*, *temp* $\times$ *diel* and *temp* $\times$ *alt* variables. All explanatory variables, including the *temp* $\times$ *rainy* variable, were selected by the top models in the early-summer (deviance = -686.43, $p < 0.001$), summer (deviance = -1257.50, $p < 0.001$) and fall (deviance = -514.23, $p < 0.001$) analyses. The results revealed the temperature-mediated seasonal and altitudinal variations in roe deer's activity patterns.

Temperature had negative effects on roe deer activity in spring, early summer and fall (spring: log-odds = -0.09, $p = 0.01$; early summer: log-odds = -0.08, $p < 0.001$; fall: log-odds = -0.11, $p < 0.001$). In summer and early fall, temperature's marginal effect was not significantly negative (summer: log-odds = -0.05, $p = 0.32$; early fall: log-odds = 0.14, $p = 0.24$). Temperature's impact on activity level interacted with the diel period and potentially led to the seasonal variations in the roe deer's activity patterns. During spring, temperature's effect was significantly negative at dawn and dusk (activity-level trend for dawn: mean = -0.08, $p = 0.03$;

dusk: mean = -0.06, $p = 0.02$) but not at day and night (day: mean = 0.01, $p = 0.74$; night: mean = 0.00, $p = 0.96$). The activity level at dusk exceeded that at the others during cold days of spring but the difference diminished as temperature increased. During early summer, temperature's effect was negative at the day and dusk (day: mean = -0.13, $p < 0.001$; dusk: mean = -0.09, $p < 0.001$) but not at dawn and night (dawn: mean = -0.03, $p = 0.14$; night: mean = 0.00, $p = 0.92$). This reveals that the activity level during the warm hours of the day, including day and dusk, decreased as temperature increased during early summer. During summer, the all-day activity level was negatively affected by temperature (dawn: mean = -0.08, $p = 0.02$; day: mean = -0.09, $p < 0.001$; dusk: mean = -0.18, $p < 0.001$; night: mean = -0.05, $p = 0.02$). The hot weather during summer potentially restrained roe deer activity. Consequently, roe deer activity exhibited nocturnal patterns in summer. During early fall, temperature's effects were negative during the day, at dusk and at night (day: mean = -0.24, $p < 0.001$; dusk: mean = -0.50, $p < 0.001$; night: mean = -0.19, $p = 0.02$) but not at dawn (dawn: mean = 0.13, $p = 0.10$). During fall, temperature's

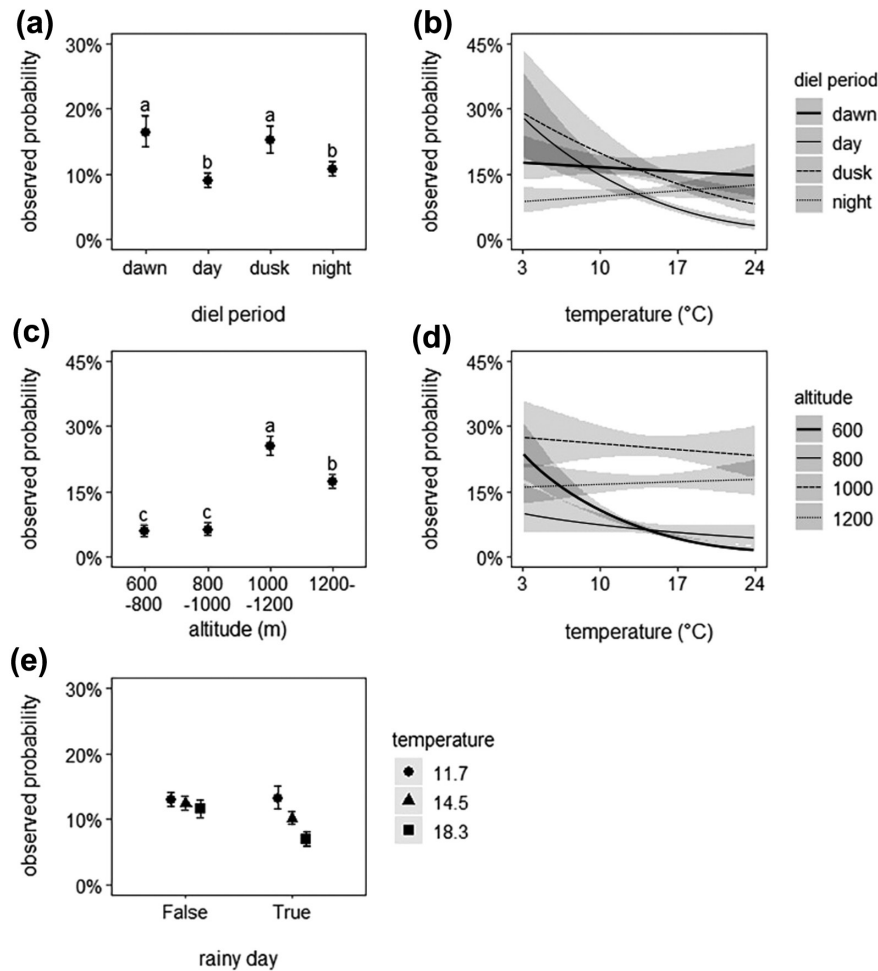


Figure 2. Effects of (a) diel period, (b) interaction between diel period and temperature, (c) altitude, (d) interaction between altitude and temperature and (e) rainy day on the observed probability of Siberian roe deer *Capreolus pygargus* in Mt Gariwang, Pyeongchang, South Korea during early summer (16 May–30 June) based on logistic regression.

effect was negative at the day (day: mean = -0.05 , $p = 0.04$) but positive at dawn, dusk and night (dawn: mean = 0.02 , $p = 0.39$; dusk: mean = 0.07 , $p < 0.01$; night: mean = 0.12 , $p < 0.001$). These findings indicate temperatures during fall potentially restrain roe deer activity at dusk and night.

Altitudinal variations in roe deer activity varied across seasons. In spring, early summer and fall, the activity level at high altitudes area (> 1000 m a.s.l.) exceeded that at low altitudes (< 1000 m a.s.l.). In summer and early fall, the activity level in areas located 800–1200 m a.s.l. exceeded that in other sites. In addition, temperature's effects on the activity level differed across altitudes. It had a negative effect on the activity level at high altitudes exclusively in summer and early fall (activity-level trends for sites located 1000–1200 m a.s.l. during spring: mean = 0.04 , $p = 0.09$; early summer: mean = -0.02 , $p = 0.13$; summer: mean = -0.06 , $p = 0.02$; early fall: mean = -0.25 , $p < 0.001$; fall: mean = -0.03 , $p = 0.24$; activity-level trends for site located > 1200 m a.s.l. during spring: mean = -0.03 , $p = 0.09$; early summer: mean = -0.01 , $p = 0.46$; summer: mean = -0.13 , $p < 0.001$;

early fall: mean = -0.27 , $p < 0.001$ and fall: mean = 0.02 , $p = 0.37$). The activity level in low-altitude areas was negatively affected by temperature throughout the study period, except at site located 800–1000 m a.s.l. in early fall and fall (activity-level trends for sites located 600–800 m a.s.l. during spring: mean = -0.05 , $p = 0.02$; early summer: mean = -0.17 , $p < 0.001$; summer: mean = -0.08 , $p = 0.01$; early fall: mean = -0.19 , $p = 0.05$; fall: mean = -0.05 , $p = 0.05$; activity-level trends for sites located 800–1000 m a.s.l. during spring: mean = -0.07 , $p = 0.01$; early summer: mean = -0.06 , $p = 0.04$; summer: mean = -0.12 , $p < 0.001$). In areas located 800–1000 m a.s.l., temperature did not have a significant effect on the activity level during early fall (mean = -0.07 , $p = 0.16$) but had a positive effect during fall (mean = 0.22 , $p < 0.001$). This reveals that the activity level in areas situated 800–1000 m a.s.l. diminished with decreasing temperatures during fall.

The effect of rainy days varied across seasons and were affected by temperature. Rainy days increased roe deer activity in early summer (log-odds of rainy day in early summer:

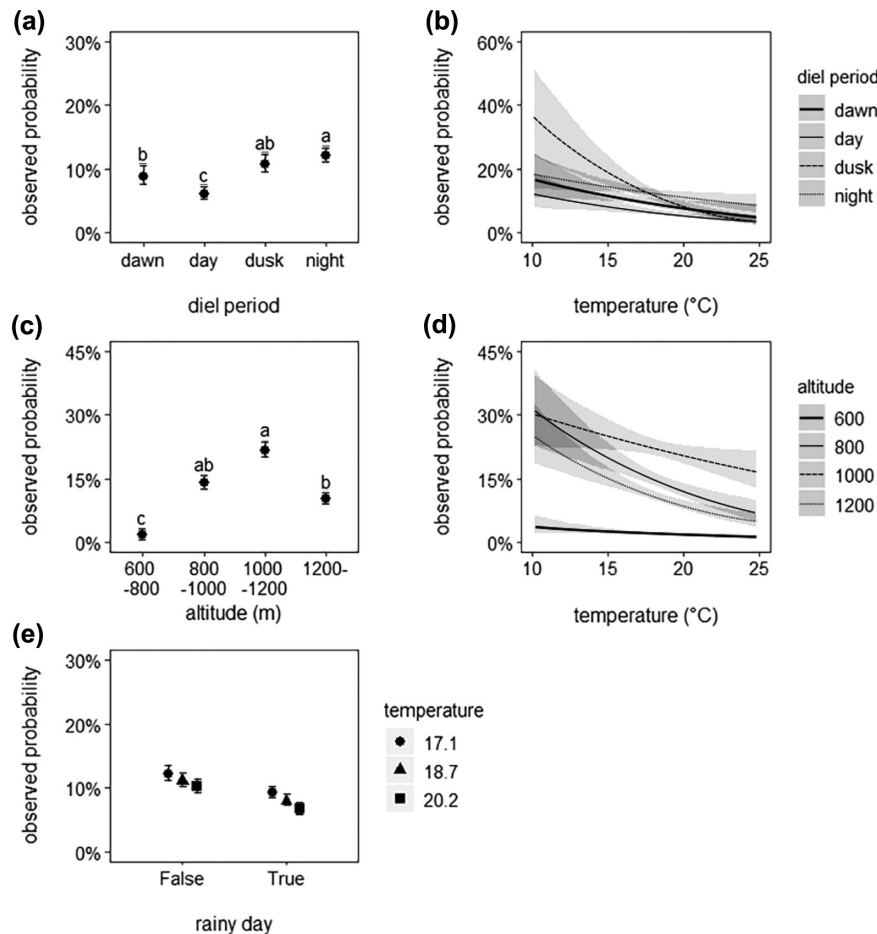


Figure 3. Effects of (a) diel period, (b) interaction between diel period and temperature, (c) altitude, (d) interaction between altitude and temperature and (e) rainy day on the observed probability of Siberian roe deer *Capreolus pygargus* in Mt Gariwang, Pyeongchang, South Korea during summer (1 July–31 August) based on logistic regression.

log-odds=1.07, $p < 0.001$) but decreased it in early fall and fall (early fall: log-odds=−0.35, $p < 0.01$; fall: log-odds=−1.12, $p < 0.01$). The interaction between rainy day and temperature had a significant effect during early summer and summer (early summer: log-odds=−0.09, $p < 0.001$; summer: log-odds=0.08, $p = 0.02$).

Discussion

Seasonal changes in temperature and deer activity patterns

Bimodal activity patterns of ruminant species, possessing two peaks at dawn and dusk, are determined based on the feeding activity. The ‘rumen fill theory’ explains the ultradian rhythms of ruminants (Moen 1973). Ruminants require ruminating time after feeding, and this usually results in their activity pattern alternating between activity and rest (Jeppesen 1989). Thus, total activity level of roe deer depends on their energy demands accordingly (Berger et al. 2002). This potentially leads to the negative relationship between

temperature and deer activity level to meet their thermoregulatory cost (Pagon et al. 2013). Moreover, this study excluded winter, during which harsh weather restrains deer activity. This might have resulted in temperature’s negative effect.

Concentrate selectors, including roe deer, prefer consuming low-fibre forage, not requiring lengthy digestion, due to a relatively small-sized rumen (Barančková et al. 2010). Such ultradian rhythms of concentrate selection offers the flexibility to adjust the activity pattern to other environmental factors, including season and temperature. Roe deer’s activity pattern depends on season and is affected by the thermoperiod (Jeppesen 1989, Pagon et al. 2013). In this study, it displayed a crepuscular pattern in spring, early summer, early fall and fall. A difference in activity pattern was noted between cool seasons, including spring and fall, and transitional seasons, including early summer and early fall. Roe deer activity exhibited the highest peak at dusk during the cool seasons but did not differ between dawn and dusk during the transitional seasons. To meet a greater thermoregulatory cost in the cool seasons, roe deer need to spend more time foraging (Berger et al. 2002). Thus, they might prefer foraging at dusk when it was warmer than at dawn.

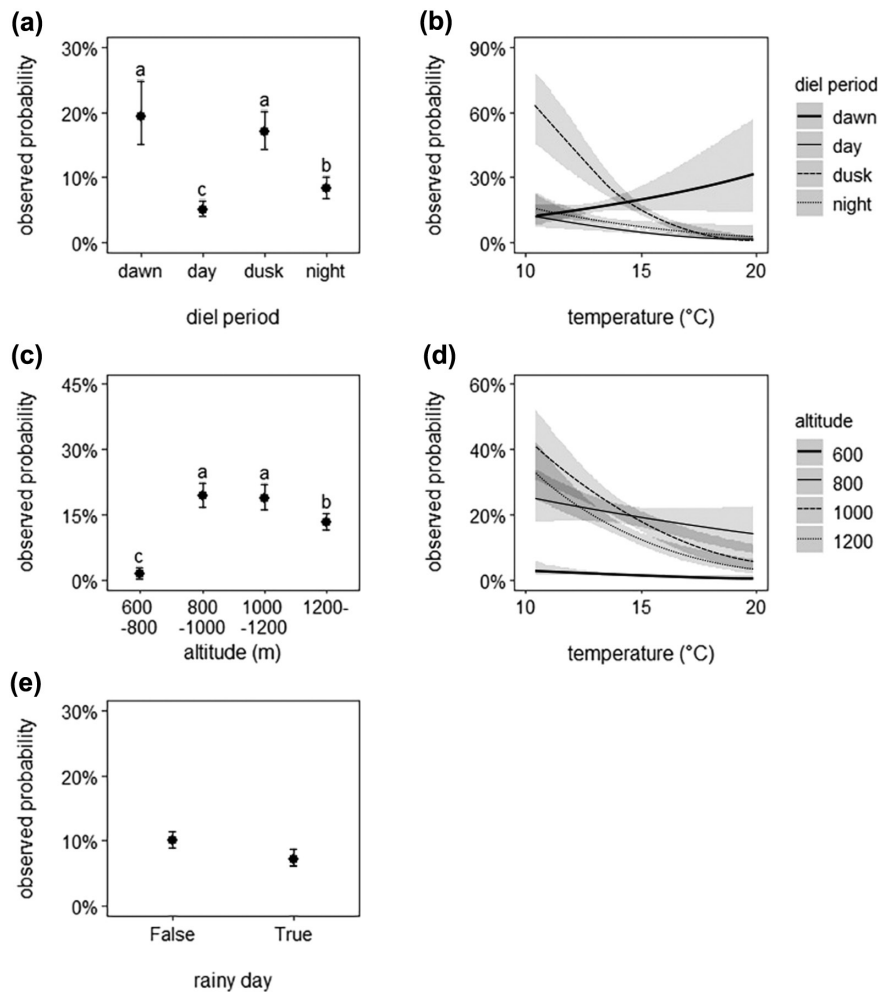


Figure 4. Effects of (a) diel period, (b) interaction between diel period and temperature, (c) altitude, (d) interaction between altitude and temperature and (e) rainy day on the observed probability of Siberian roe deer *Capreolus pygargus* in Mt Gariwang, Pyeongchang, South Korea during early fall (September) based on logistic regression.

During summer, heat stress caused roe deer activity pattern to change from crepuscular to nocturnal. High temperatures potentially restrained deer's diurnal activity and favoured their nocturnal activity during summer, and this finding has been corroborated by previous studies on deer's nocturnal activity during summer (Ikeda et al. 2015, 2016). In addition, the absence of a nocturnal predator inevitably favoured roe deer's nocturnal activity in the study area. Interspecific interaction is one of the most important factors determining deer's temporal niche (Ikeda et al. 2016, Higdon et al. 2019). In the study area, yellow-throated marten was an opportunistic predator for roe deer, and this diurnal species would not restrain roe deer's nocturnal activity.

The effect of weather condition, e.g. rainfall and wind, mediates by temperature and it, thus, show inconsistent impact on deer's activity (Kamler et al. 2007, Ikeda et al. 2015). In this study, effect of rainy days on roe deer's activity was distinct among seasons. Throughout early fall and fall, roe deer's activity decreased on rainy days, likely to maintain their body temperature. Conversely, during early summer, their

activity level increased on rainy days due to reduced heat stress. However, the positive effect of rainy days was not observed during summer, the hottest season. As roe deer reduced heat stress by changing their activity pattern to nocturnal, the rainy day might have a less pronounced impact on their activities.

Altitudinal variations in resource availability, interspecific interaction and deer activity

Roe deer's altitudinal preferences reportedly differ with habitat conditions (Mysterud 1999, Qin 2011, Park and Lee 2014). In this study, roe deer tended to occupy high-altitude areas above 800–1000 m a.s.l.. Altitude can affect roe deer's ecology in several ways, including changes in microclimate (Mysterud et al. 1997, Pagon et al. 2013). Temperature is generally lower at higher altitudes, as previously observed in the study area (Lee et al. 2023). Accordingly, temperature's effect depended on altitude. In low-altitude areas, higher temperatures were found to reduce roe deer's activity level throughout the study period. In contrast, temperature's

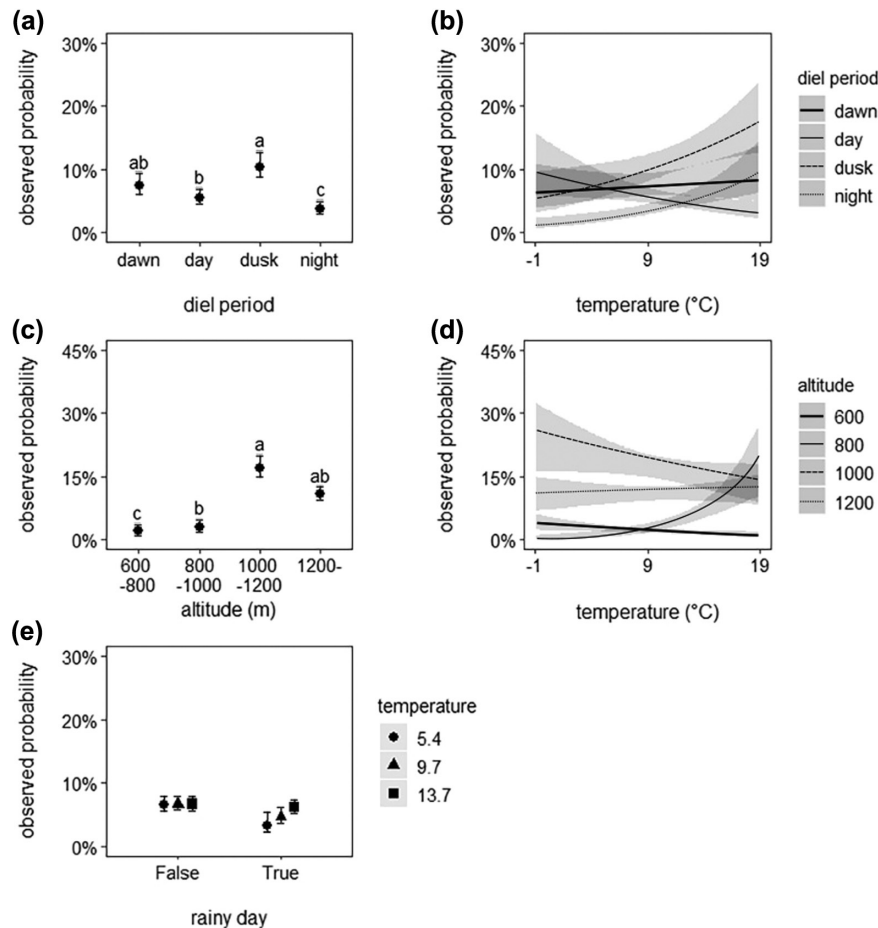


Figure 5. Effects of (a) diel period, (b) interaction between diel period and temperature, (c) altitude, (d) interaction between altitude and temperature and (e) rainy day on the observed probability of Siberian roe deer *Capreolus pygargus* in Mt Gariwang, Pyeongchang, South Korea during fall (October) based on logistic regression.

negative effect was exclusively observed from summer to early fall in high-altitude areas, indicating that the lower temperatures at high altitudes may be more favourable roe deer activity than those of low altitudes (Carvalho et al. 2008). Thus, the higher activity level in high-altitude areas may result from roe deer's thermoregulatory behaviour.

During summer, roe deer's activity level was the highest in areas located 800–1200 m a.s.l., while roe deer preferred to use higher altitudes (> 1000 m a.s.l.), during the other seasons. The roe deer's transition to lower altitudes in summer may be influenced by resource availability (Igota et al. 2004, Adhikari et al. 2016), which is a major determinant of deer distribution (Mysterud et al. 1999, van Beest et al. 2010). A previous study in this area revealed that understory vegetation decreased as altitude increased (Lee et al. 2022). For roe deer, understory vegetation is the most important survival resource, providing food and cover (Mysterud and Østbye 1999). The negative correlation between resource availability and altitude is inevitably most pronounced during summer due to rapid vegetation growth. This potentially affected roe deer activity in summer and early fall. In this study, roe deer tended to move to lower altitudes in summer and early fall,

returning to higher altitudes in fall when forage had become scarce. This suggests that resource availability plays a significant role in roe deer's seasonal movement (Igota et al. 2004, Carvalho et al. 2008). Roe deer movement towards lower-altitude areas during the hottest season may be attributed to nocturnal activity patterns that reduced heat stress.

Deer distribution is affected by interspecific interactions, including competition and predation (Hopcraft et al. 2010, Ferretti and Fattorini 2021). When competitor or predator distribution is dependent on altitude, altitudinal patterns in deer distribution can occur (Pagon et al. 2013). In addition, these interspecific interactions can vary seasonally, depending on the occurrence of species (Smolko et al. 2018). In the study area, water deer were predominantly in low-altitude areas (< 1000 m a.s.l.) during spring and early summer, exhibiting consistency with a previous study's findings wherein water deer preferred low-elevation forest edges in South Korea (Eom et al. 2019). This suggests that interspecific competition may occur between two deer species in low-altitude areas during spring and early summer. Roe deer may avoid low-altitude areas to evade competition with water deer during spring and early summer (Eom et al. 2023a).

We examined the seasonal patterns in roe deer activity and altitudinal distribution from spring to fall. These patterns were influenced by a complex interplay of various factors, including season, microclimate, resource availability and interspecific interaction. In this study, roe deer coped with heat stress during summer by modifying their diel activity patterns, allowing them to shift towards lower altitude areas to find more resources. The roe deer's behavioural strategies lessened the impact of high temperatures on roe deer, potentially aiding in their adaptation to the rising temperature in montane habitats resulting from climate change. This study's finding suggests the importance of species' behavioural flexibility in mediating their response to changing environmental conditions, including climate change, and may contribute to their long-term survival in challenging climates.

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Author contributions

Tae-Kyung Eom: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jae-Kang Lee:** Formal analysis (equal); Investigation (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Dong-Ho Lee:** Formal analysis (equal); Investigation (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Hyeongyu Ko:** Investigation (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Shin-Jae Rhim:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mkkwh715x> (Eom et al. 2023b).

Supporting information

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

References

Adhikari, P., Park, S. M., Kim, T. W., Lee, J. W., Kim, G. R., Han, S. H. and Oh, H. S. 2016. Seasonal and altitudinal variation in roe deer (*Capreolus pygargus tianschanicus*) diet on Jeju Island, South Korea. – *J. Asia Pac. Biodivers.* 9: 422–428.

Barančková, M., Krojerová-Prokešová, J., Šustr, P. and Heurich, M. 2010. Annual changes in roe deer (*Capreolus capreolus* L.) diet in the Bohemian forest, Czech Republic/Germany. – *Eur. J. Wildl. Res.* 56: 327–333.

Benjamin, C. S., Uphus, L., Lüpke, M., Rojas-Botero, S., Dhillon, M. S., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Redlich, S., Riebl, R., Tobisch, C., Uhler, J., Zhang, J., Menzel, A. and Peters, W. 2022. Modelling the relative abundance of roe deer (*Capreolus capreolus* L.) along a climate and land-use gradient. – *Animals (Basel)* 12: 222.

Berger, A., Scheibe, K.-M., Brelurut, A., Schober, F. and Streich, W. J. 2002. Seasonal variation of diurnal and ultradian rhythms in red deer. – *Biol. Rhythm Res.* 33: 237–253.

Bojarska, K., Kurek, K., Śnieżko, S., Wierzbowska, I., Król, W., Zysk-Gorczyńska, E., Baś, G., Widera, E. and Okarma, H. 2020. Winter severity and anthropogenic factors affect spatial behaviour of red deer in the Carpathians. – *Mamm. Res.* 65: 815–823.

Brinkman, T. J., Deperno, C. S., Jenks, J. A., Haroldson, B. S. and Osborn, R. G. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. – *J. Wildl. Manage.* 69: 1099–1111.

Carvalho, P., Nogueira, A. J. A., Soares, A. M. V. M. and Fonseca, C. 2008. Ranging behaviour of translocated roe deer in a Mediterranean habitat: seasonal and altitudinal influences on home range size and patterns of range use. – *Mammalia* 72: 89–94.

Davis, M. L., Stephens, P. A. and Kjellander, P. 2016. Beyond climate envelope projections: roe deer survival and environmental change. – *J. Wildl. Manage.* 80: 452–464.

Eom, T. K., Hwang, H. S., Lee, J. K. and Rhim, S. J. 2019. Influence of topography on the summer habitat use by the Korean water deer *Hydropotes inermis argyropus* Heude, 1884 (Artiodactyla: Cervidae) in a low-mountainous area. – *Acta Zool. Bulg.* 71: 537–544.

Eom, T. K., Lee, J. K., Lee, D. H., Bae, H. K., Ko, H., Kim, K. J., Jung, S. C., Lim, J. H. and Rhim, S. J. 2023a. Temporal niche overlap of medium sized herbivores in the Seoraksan and Jirisan National park, South Korea. – *Pak. J. Zool.* 55: 1003–1008.

Eom, T. K., Lee, J. K., Lee, D. H., Ko, H. and Rhim, S. J. 2023b. Data from: Adaptive response of Siberian roe deer *Capreolus pygargus* to climate and altitude in the temperate forests of South Korea. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.mkkwh715x>.

Ferretti, F. and Fattorini, N. 2021. Competitor densities, habitat, and weather: effects on interspecific interactions between wild deer species. – *Integr. Zool.* 16: 670–684.

Higdon, S. D., Diggins, C. A., Cherry, M. J. and Ford, W. M. 2019. Activity patterns and temporal predator avoidance of white-tailed deer (*Odocoileus virginianus*) during the fawning season. – *J. Ethol.* 37: 283–290.

Hopcraft, J. G. C., Olff, H. and Sinclair, A. R. E. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. – *Trends Ecol. Evol.* 25: 119–128.

Igota, H., Sakuragi, M., Uno, H., Kaji, K., Kaneko, M., Akamatsu, R. and Maekawa, K. 2004. Seasonal migration patterns of female sika deer in eastern Hokkaido, Japan. – *Ecol. Res.* 19: 169–178.

Ikeda, T., Takahashi, H., Yoshida, T., Igota, H., Matsuura, Y., Take-shita, K. and Kaji, K. 2015. Seasonal variation of activity pat-

- tern in sika deer (*Cervus nippon*) as assessed by camera trap survey. – *Mamm. Study* 40: 199–205.
- Ikeda, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K. and Koizumi, I. 2016. Seasonal and diel activity patterns of eight sympatric mammals in northern Japan revealed by an intensive camera-trap survey. – *PLoS One* 11: e0163602.
- Jasińska, K. D., Jackowiak, M., Gryz, J., Bijak, S., Szyc, K. and Krauze-Gryz, D. 2021. Habitat-related differences in winter presence and spring-summer activity of roe deer in Warsaw. – *Forests* 12: 970.
- Jeppesen, J. L. 1989. Activity patterns of free-ranging roe deer (*Capreolus capreolus*) at Kalø. – *Dan. Rev. Game Biol.* 13: 1–30.
- Jiang, F., Zhang, J., Gao, H., Cai, Z., Zhou, X., Li, S. and Zhang, T. 2020. Musk deer (*Moschus* spp.) face redistribution to higher elevations and latitudes under climate change in China. – *Sci. Total Environ.* 704: 135335.
- Kamal, J. F., Jędrzejewska, B. and Jędrzejewski, W. 2007. Activity patterns of red deer in Białowieża national park, Poland. – *J. Mammal.* 88: 508–514.
- Lee, J. K., Eom, T. K., Bae, H. K., Lee, D. H. and Rhim, S. J. 2022. Responsive strategies of three sympatric small rodents to the altitudinal effects on microhabitats. – *Anim. Biol.* 72: 63–77.
- Lee, J. K., Eom, T. K., Lee, D. H., Ko, H. and Rhim, S. J. 2023. Effects of multiple ecological factors on the body mass of small rodents in a forest ecosystem. – *Wildl. Biol.* 2023: e01078.
- Lenth, R. 2022. emmeans: estimated marginal means, aka least-squares means. – <https://CRAN.R-project.org/package=emmeans>.
- Levinsky, I., Skov, F., Svenning, J. C. and Rahbek, C. 2007. Potential impacts of climate change on the distributions and diversity patterns of European mammals. – *Biodivers. Conserv.* 16: 3803–3816.
- Moen, A. N. 1973. *Wildlife ecology*. – W.H. Freeman and Company.
- Muñoz-Delgado, J., Corsi-Cabrera, M., Canales-Espinosa, D., Santillán-Doherty, A. M. and Erkert, H. G. 2004. Astronomical and meteorological parameters and rest-activity rhythm in the spider monkey *Ateles geoffroyi*. – *Physiol. Behav.* 83: 107–117.
- Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. – *J. Zool.* 247: 479–486.
- Mysterud, A. and Østbye, E. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. – *Wildl. Soc. Bull.* 27: 385–394.
- Mysterud, A., Bjørnsen, B. H. and Østbye, E. 1997. Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. – *Wildl. Biol.* 3: 27–33.
- Mysterud, A., Lian, L. B. and Hjermann, D. Ø. 1999. Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. – *Can. J. Zool.* 77: 1486–1493.
- Pagon, N., Grignolio, S., Pipia, A., Bongi, P., Bertolucci, C. and Apollonio, M. 2013. Seasonal variation of activity patterns in roe deer in a temperate forested area. – *Chronobiol. Int.* 30: 772–785.
- Park, Y. S. and Lee, W. S. 2014. Characteristics of habitat-using of Siberian roe deer in Seoraksan (MT) national park. – *J. Kor. Soc. Environ. Restor. Technol.* 17: 91–109.
- Qin, X. 2011. Summer bed-site selection by roe deer in a predator free area. – *Ital. J. Mamm.* 22: 269–279.
- Schweiger, B. R. and Frey, J. K. 2021. Weather determines daily activity pattern of an endemic chipmunk with predictions for climate change. – *Clim. Change Ecol.* 2: 100027.
- Signer, C., Ruf, T. and Arnold, W. 2011. Hypometabolism and basking: the strategies of alpine ibex to endure harsh overwintering conditions. – *Funct. Ecol.* 25: 537–547.
- Smolko, P., Kropil, R., Pataky, T., Veselovská, A. and Merrill, E. 2018. Why do migrants move downhill? The effects of increasing predation and density on red deer altitudinal migration in temperate Carpathian forests. – *Mamm. Res.* 63: 297–305.
- Son, S. H., Hwang, H. S., Lee, J. K., Eom, T. K., Park, C. R., Lee, E. J., Kang, J. H. and Rhim, S. J. 2017. Influence of tree thinning on the abundance of mammals in a Japanese larch *Larix kaempferi* plantation. – *Anim. Cells Syst. (Seoul)* 21: 70–75.
- van Beest, F. M., Mysterud, A., Loe, L. E. and Milner, J. M. 2010. Forage quantity, quality and depletion as scaledependent mechanisms driving habitat selection of a large browsing herbivore. – *J. Anim. Ecol.* 79: 910–922.
- Weiskopf, S. R., Ledee, O. E. and Thompson, L. M. 2019. Climate change effects on deer and moose in the midwest. – *J. Wildl. Manage.* 83: 769–781.
- Yusefi, G. H., Safi, K., Tarroso, P. and Brito, J. C. 2021. The impacts of extreme climate change on mammals differ among functional groups at regional scale: the case of Iranian terrestrial mammals. – *Divers. Distrib.* 27: 1634–1647.
- Zhou, W., Wang, M., Gao, K., Gao, H., Wei, F. and Nie, Y. 2022. Behavioural thermoregulation by montane ungulates under climate warming. – *Divers. Distrib.* 28: 2229–2238.