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Variation of rodents' body temperature across elevation in Alps

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ABSTRACT

Understanding the physiological adaptations of animals living in mountain landscapes is a key to predicting the responses of individuals to environmental changes, especially those imposed by climate. In this regard, the mechanism of body temperature regulation is particularly important in determining the physiological limits for activity under hypoxic and climatic stressful conditions. Numerous studies have shown that body temperature of rodents and other animals decreases with elevation and with extreme winter temperatures. But surprisingly, it is still not known how body temperature of wild animals varies along elevation during their reproductive seasons. We studied variation in core body temperature among individuals (N = 294) of four rodent species (*Apodemus flavicollis*, *Apodemus sylvaticus*, *Apodemus alpicola*, *Myodes glareolus*) and its association with elevation (from 400 to 1,822 m asl), accounting for variation in environment temperature, microhabitat structure, body condition, and sex. Results showed a strong positive effect of elevation

and a more limited effect of environmental temperature on rodents' body temperature during spring and summer. The effect of elevation on body temperature was influenced neither by interactions with environmental temperature or sex nor by the microhabitat structure. We suggest that in normothermic condition at high elevations, small mammals experiencing hypoxic exposure might show physiological adjustments for increasing efficiency of thermoregulation in low oxygen conditions.

Keywords: adaptation, altitude, hypoxia, heterotermy, normothermia, rodents

INTRODUCTION

Regulation of body temperature (T_b) is a key aspect of endothermic physiology (Hankenson et al. 2018), where animals maintain high and relatively stable core temperature optimizing cellular physiological processes (Chappell et al. 2007). Individual temperature varies between and within species, and this variation can reflect adaptive and plastic responses to environmental heterogeneity (Heinrich 1977; Geiser 2004; Angilletta et al. 2010). Over the past years, evidence has accumulated describing variable physiological mechanisms across elevational gradients (Careau 2012; Cheviron et al. 2012, 2013; Dzal 2018). High altitudes are characterized by decreased ambient temperatures and oxygen partial pressure (Storz et al. 2010), challenging animals' T_b regulation (Tattersall and Milsom 2009). Animals of relatively small bodies (!100 g), such as many mammals and birds, are under increased pressure because of their high surface-to-volume ratio, resulting in high relative energetic demands to support temperature regulation (Robertson et al. 2019).

In mountains, air temperature decreases by approximately 0.55 C°–0.65 C° every 100 m of altitude increase (Anslow and Shawn 2002). Animals adapted to high altitudes and exposed to cold environments may apply physiological adjustments to increase heat production, or thermogenesis (e.g., by increased vascularization of brown adipose tissue and upregulation of mitochondrial thermogenic respiration; Shabalina et al. 2013). Maintaining high T_b by endothermic mechanisms

under low air temperatures is physiologically costly and depends on the degree and duration of cold exposure and habitat productivity (Bastos et al. 2021). Hypoxic conditions can further limit T_b regulation, as the exposure to decreased partial pressure of oxygen can limit aerobic physiology (Chappell and Snyder 1984; Cadena and Tattersall 2014). T_b also has a clear sex-dependent pattern in response to environmental constraints. For instance, post pubertal female mice can have 0.2 C° – 0.5 C° higher temperatures than male mice (Marques et al. 2017). However, it is not clear how sexual differences in T_b can interact with plastic and adaptive responses to other factors, such as elevation (Marques et al. 2017).

Endothermic thermoregulation physiology demands a high amount of energy to maintain a stable and high T_b (Wooden and Walsberg 2002). Vegetation provides important food resources and habitat for rodents, and T_b regulation may be affected by fluctuation in availability of food resources (Bastos et al. 2021). Fluctuating and harsh conditions at high altitudes result in lower plant diversity and coverage (Nor 2001) and reduced seed production (Hodkinson 2008). Decreased food diversity, abundance, and predictability and shelter availability expose rodents to nutrients restriction and variable air temperatures (Nagy and Grabherr 2009; Camacho et al. 2019). In response to these environmental challenges, animals may adopt an effective energy-saving strategy, such as daily torpor, which can reduce energy expenditures (Ruf and Geiser 2015). Despite the many factors that may affect T_b in animals living across altitudes, surprisingly few studies have collected data at the individual level and tested how environmental and individual predictors affect variation in T_b in the wild (but see, e.g., Boratyński et al. 2021).

Here, we studied variation in T_b in four rodent species across a moderate altitudinal gradient in the Alps during their reproductive season. In high altitudes, individuals are exposed to decreasing air temperature and oxygen partial pressure. If air temperature influences rodents' T_b, it can be predicted that individuals inhabiting higher altitudes would have higher T_b (i.e., as a result of

increased heat production). On the other hand, when air temperature becomes too low, animals from high altitudes could evolve low T_b to decrease the body-environment temperature gradient and costs of homeothermic thermoregulation. We also predicted that a sex-dependent pattern of T_b and habitat variation, such as slope exposure and plant diversity, richness, and coverage, could further modulate the elevation effects.

MATERIAL AND METHODS

Study Area

The study area was located in Piedmont region (north-western Italy), within the territory of the Gran Paradiso National Park, in the Graian Alps (fig. 1, top). We identified 12 trapping locations distanced at least 5 km from each other, spanned across a moderate elevational gradient, from 400 to 1,822 m asl (fig. 1, bottom). Deciduous forests, at low elevations (400–1,000m), were composed of European beech (*Fagus sylvatica*), followed by sycamore maple (*Acer pseudoplatanus*), large-leaved linden (*Tilia platyphyllos*), European ash (*Fraxinus excelsior*), *Populus* spp., *Betula* spp., and chestnut (*Castanea sativa*). Mixed forests, at mid elevations (1,000–1,800 m), were composed of species belonging to deciduous and coniferous trees. Coniferous forests, at high elevations (1,800–2,000 m), were dominated by larch (*Larix decidua*), often mixed with European spruce (*Picea abies*)

Trapping and Handling of Animals

Trapping was conducted during the breeding season of the target species, from April 15 to September 15, 2020. Days of trapping at high- and low-altitude sites were randomly alternated, and the order of trapping was recorded. Each trapping location consisted of a line of 30 live traps (Sherman traps, 229 mm x 89 mm x 76 mm in size) located every 10 m. Traps were set at sunset and inspected at sunrise. Each trapping session lasted 1 wk. Traps were baited with apple, sunflower

seeds, and peanut butter, and cotton was provided as bedding. Trapped animals were marked with fur clipping and weighed. Adult individuals of the trapped species (based on fur characteristics and body dimensions; e.g., Gurnell and Flowerdew 2019 — yellow-necked mouse (*Apodemus flavicollis*), wood mouse (*Apodemus sylvaticus*), alpine field mouse (*Apodemus alpicola*), and bank vole (*Myodes glareolus*) — with a minimum body weight of 15 g for *Apodemus* spp. and 13 g for *M. glareolus* were transported to the laboratory (fig. 1, top), kept in individual cages, and provided with water.

Rectal T_b was measured on postabsorptive animals acclimatized to laboratory conditions for approximately 14 h. T_b was measured during the active phase of the species' daily cycle, around 10:00 p.m. on the same day of capture. A rectal thermocouple (RET-3; accuracy: ± 0.1 C°) connected to the thermometer (model PST095) was inserted 2 cm into the animal's rectum for

10 s. Animals with T_b < 35 °C (eight individuals probably in hypothermic condition) or T_b > 41 °C (one individual who may have suffered from fever) were excluded from analyses. Animal's sex was recorded, along with body weight (Pesola spring balance; 51 g) and head width and head, ear, foot, body, and tail lengths measured with calipers (Mitutoyo 530–119 calipers; ± 0.02 mm). Tissue ear samples were collected and used in genetic bar coding of the *Apodemus* species. Animals were kept for no more than 24 h and then released to the location of capture. All experimental procedures were approved by the national bioethical committee (Ministry for Health, 618/2020-PR; Institute for Environmental Protection and Research, protocol 13486 del 23/3/2020), and trapping and handling of animals were authorized by the Gran Paradiso National Park (0003037/2020 of 18/08/2020) and the Province of Turin (618/2020-PR).

Environmental Data

Daily minimum air temperature was selected as the probable driving variable for T_b adaptation in nocturnal animals to estimate thermal stress. We obtained these data from a meteorological database available online (ARPA Piedmont; http://www.arpa.piemonte.it). Eight of 12 weather stations were located within 2 km of and at the same altitude as the trapping sites. The remaining four weather stations were located within 5 km of and at the same altitude as the trapping sites (fig. 1, top). Mean values of daily minimum air temperature (TEmean) for 30 d before trappings were used in the analysis.

The number of shrub and tree species was included in the analyses to account for variation in plant richness. The percentage of shrub and tree species coverage was calculated to account for variation in plant diversity and vegetation coverage. We collected vegetation data in seven plots located within the trapping line: the first plot was centered around the first trap, and the following plots were placed every five traps. Each plot was constituted by a 5 x 5-m square with a live trap located in the center. The tree/bush species present in the plot were identified, and cover of each species was estimated visually.

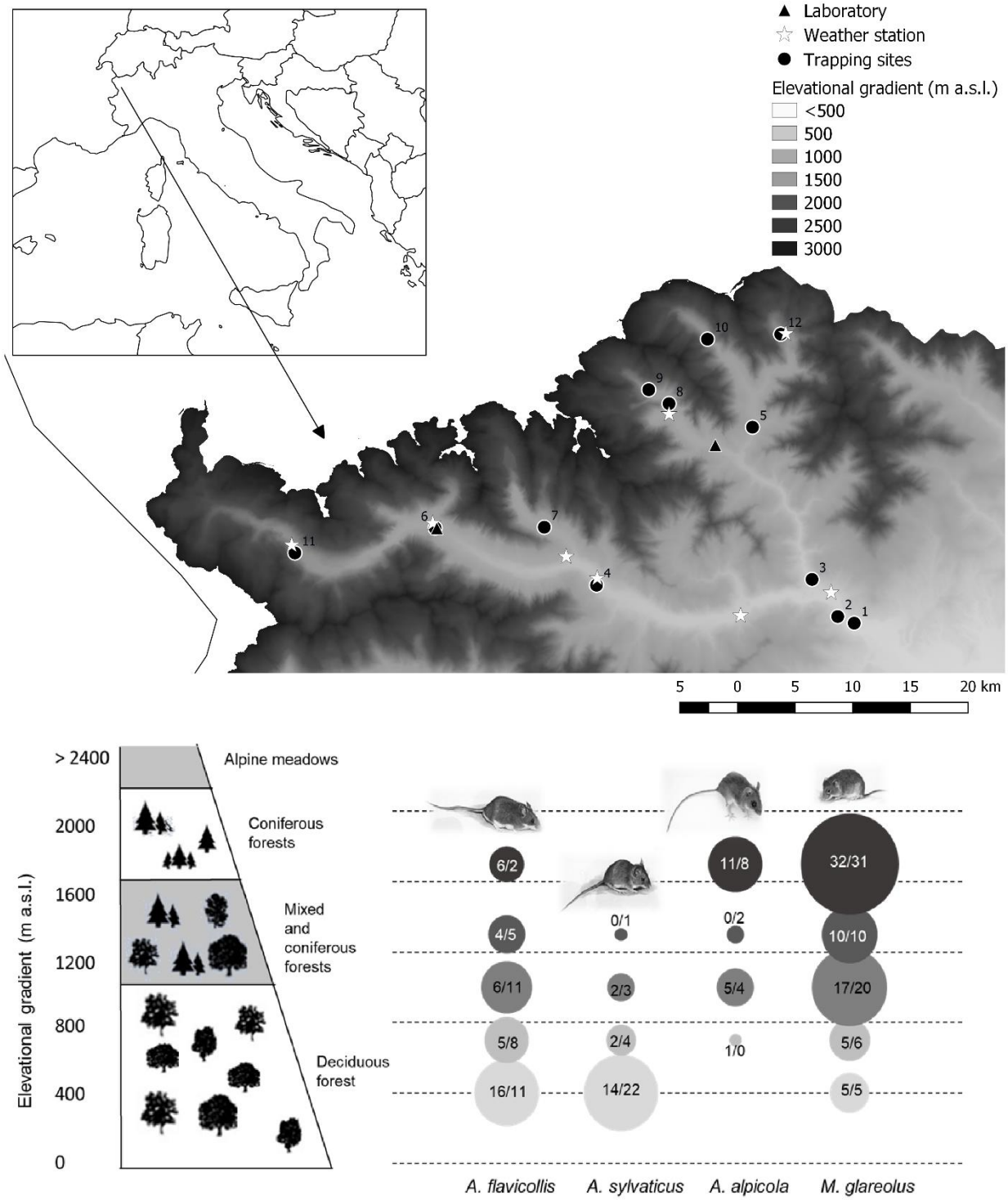

Figure 1. Top, location of the Gran Paradiso National Park (45° 31′ 7.02″ N, 7° 16′ 2.22″ E) and the 12 trapping sites, weather stations, and laboratories (table A1). Bottom, habitats (deciduous, mixed, and coniferous forests) and species (*Apodemus flavicollis*, *Apodemus sylvaticus*, *Apodemus alpicola*, and *Myodes glareolus*) studied across an elevational gradient (400–1,822 m asl) and numbers of captured female/male rodents.

We assigned to each species one class of coverage out of five (<5%, 5%–25%, 25.1%–50%, 50.1%–75%, 75.1%–100%). We then calculated the midpoint of each assigned coverage class (Wikum and Shanholtzer 1978) and summed them to obtain the vegetation coverage of each trapping location. We calculated plant diversity using the Shannon diversity index (Rad et al. 2009). To calculate the proportional abundance needed for this index, we assigned a score to each coverage class (1 for <5%, 2 for 5%–25%, 3 for 25.1%–50%, 4 for 50.1%–75%, 5 for 75.1%–100%) and divided each score by the sum of the scores of all of the species at each site. Within each plot, we registered elevation (GPS Garmin eTrex 32x) and geographic exposure of the trapping site (values from 0° as north and deviation from that exposure moving clockwise and counter clockwise to 180° as maximum value as south).

Statistical Analyses

All continuous variables (T_b, elevation, TEmean, plant richness, plant diversity, vegetation coverage, and exposure) were log10 transformed before analyses to improve normality of distributions of their residuals. To assess how T_b (response variable) varied as a function of elevation, minimum environment temperature, plant richness and diversity, vegetation coverage, exposure, and sex (predictors), we applied generalized linear mixed analysis accounting for variation among trapping locations (random factor), body size (head width), and condition (continuous predictors), using the package glmmADMB (Bolker et al. 2012; R Core Team 2019).

Body condition was calculated as residual variation from body mass regressed against head width (e.g., Boratyński et al. 2010). We evaluated T_b variation across all rodent species and tested differences among species (fixed factor). We account for two seasons (spring and summer) included in this study as fixed factors. To evaluate differential responses to elevation among females and males, a two-way interaction between elevation and sex was tested. To assess whether air temperature influences response to elevation, a two-way interaction between elevation and

minimum air temperature was tested. Nonsignificant interactions were excluded from the analysis by applying a stepwise backward reduction approach. Lack of multicollinearity among predictors was confirmed with variance inflation factors (< 2.5). The best model was selected according to the lowest Akaike information criterion (Harrison et al. 2018). To test whether movement of the animals to the laboratory could have affected our results, we ran an additional analysis including the absolute difference in elevation between the laboratory and the trapping site. Such effect was insignificant (absolute elevation difference: β (SE) = -0.0129 (± 0.0115), z = -1.13, p = 0.26); therefore, it was excluded from the final analysis. To investigate consistency of detected results, separate analyses for each species were also performed.

RESULTS

T_b was measured in 294 individuals (141 females and 153 males), out of which 153 belong to the genus *Apodemus* and 141 are *Myodes glareolus* (69 females and 72 males). After genotyping, *Apodemus s*pp. were determined to be 74 *A. flavicollis* (37 females and 37 males), 48 *A. sylvaticus* (18 females and 30 males), and 31 *A. alpicola* (17 females and 14 males; fig. 1; see also fig. A1 and table A2 [fig. A1 and tables A1–A4 are available online]). Across a gradient of elevation (mean: 1,084 m asl; first quartile: 723 m asl; third quartile: 1,564 m asl), we recorded TEmean of 10.4 °C, with a difference of 4.6 °C between mean TEmean at the highest (7.7 °C) and lowest (12.3 °C) elevations. Elevation was negatively correlated with TEmean (Pearson product moment correlation: r = -0.16, p = 0.003) and positively correlated with vegetation coverage (r = 0.44, p < 0.001) and plant diversity (r = 0.19, p < 0.001), while there was no correlation with plant richness (r = 0.05, p = 0.29).

We found that rodents' T_b increased with increasing elevation (β ± SE = 0.023 ± 0.007, z = 3.53, p < 0.001; table 1; fig. 2). We also found higher T_b in females than in males (β = 0.004 ± 0.001, z =

3.85, p < 0.001; fig. 2). The interactions between elevation and TEmean (β = -0.064 ± 0.037, z = -1.75, p = 0.08) and between elevation and sex (β = -0.004 ± 0.005, z = -0.77, p = 0.44) did not affect animals' T_b. We found a positive effect of minimum environmental temperature on T_b (β = 0.027 ± 0.006, z = 5.93, p < 0.001) but only in the analysis including 10 rodents captured in April, when TEmean's were very low (tables 1, A3).

The positive covariation between T_b and elevation was detected in separate analyses for *A. flavicollis* (β = 0.020 ± 0.006, z = 3.08, p = 0.003) and *M. glareolus* (b p 0:024 5 0:008, z p 2:75, P p 0:006) β = 0.024 ± 0.008, z = 2.75, p = 0.006), but not for *A. alpicola* (β = - 0.035 ± 0.107, z = - 0.33, p = 0.74), and the effect was negative for *A. sylvaticus* (β = - 0.071 ± 0.025, z = -2.85, p = 0.007; fig. 3; table A4).

Table 1. Generalized mixed analysis to quantify effect of elevation (and other predictors) on rodents' body temperature.

	β (SE)	*z*	*p*
A. flavicollis	0.003 (0.002)	1.23	0.22
M. glareolus	0.001 (0.002)	0.38	0.70
A. sylvaticus	0.0003 (0.002)	0.11	0.91
Seasonality (1, 2)	0.001 (0.003)	0.22	0.82
Elevation	0.023 (0.007)	3.53	**< 0.001**
T_{Emean}	0.009 (0.015)	0.59	0.55
Sex (0,1)	0.004 (0.001)	3.85	**< 0.001**
Richness	0.003 (0.011)	0.27	0.78
Vegetation cover	-0.002 (0.011)	-0.24	0.80
Plant diversity	-0.001 (0.003)	-0.48	0.63
Exposure	-0.001 (0.003)	-0.27	0.78

BC	-0.007 (0.006)	-1.10	0.27
Head width	0.002 (0.019)	0.13	0.90

NOTE. The model included log10-transformed variables (elevation; mean daily minimum air temperature, TEmean; plant richness; plant diversity; vegetation coverage; exposure; head width) and body condition (BC) as continuous variables, and seasonality (1 for spring and 2 for summer), sex (1 for female, 0 for male) and species (A. flavicollis, M. glareolus, A. sylvaticus and A. alpicola) as categorical factors. Area was set as random effect: Variance = 2.4e-06, SD = 0.001549. R^2 = 0.2278; Adjusted R^2 = 0.2035.

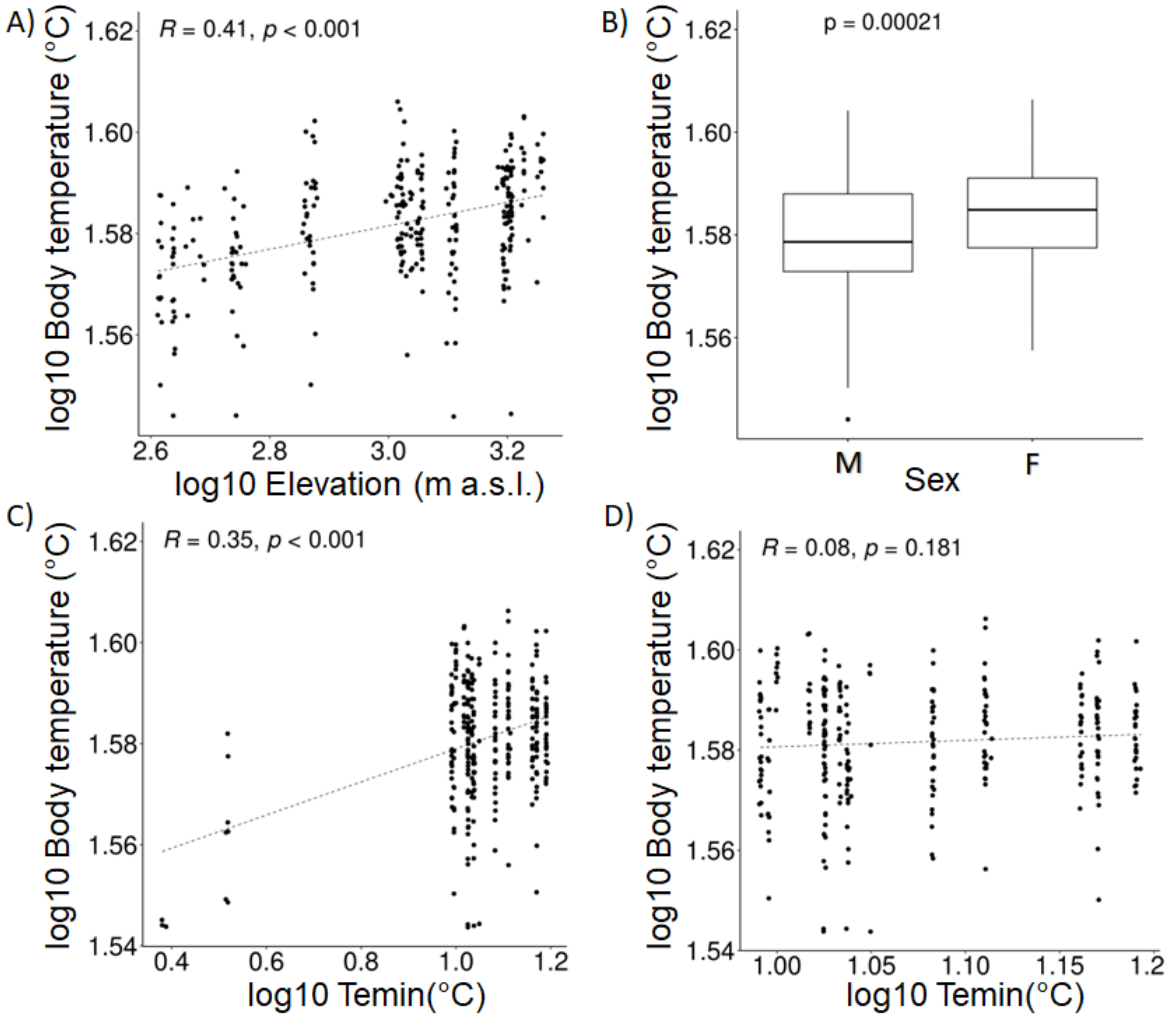

Figure 2. Variation in rodent body temperature as predicted by (A) elevation, (B) sex and daily minimum air temperature (T_{Emean}) before (C) and after (D) exclusion the lowest ten values of T_{Emean} (< 9.8 °C). Correlation coefficient and p values are reported.

We found that females have higher T_b than males in *A. flavicollis* ($\beta = 0.006 \pm 0.002$, $z = 2.53$, $p = 0.013$) and *M. glareolus* ($\beta = 0.003 \pm 0.001$, $z = 2.37$, $p = 0.018$), but not in *A. sylvaticus* ($\beta = 0.003 \pm 0.003$, $z = 1.05$, $p = 0.29$) or in *A. alpicola* ($\beta = 0.002 \pm 0.004$, $z = 0.60$, $p = 0.54$). In *A. sylvaticus* T_b positively covaried with TEmean ($\beta = 0.233 \pm 0.062$, $z = 3.75$, $p < 0.001$), and weakly negatively with plant diversity ($\beta = -0.019 \pm 0.009$, $z = -2.13$, $p = 0.040$), vegetation cover ($\beta = -0.044 \pm 0.021$, $z = -2.08$, $p = 0.044$) and positively with northern exposure ($\beta = 0.011 \pm 0.005$, $z = 2.09$, $p = 0.044$). No other environmental predictors or body size or condition affected T_b in any of the species (table A4).

DISCUSSION

To the best of our knowledge, this is the first study to evaluate how rodents' T_b varies across a moderate elevation gradient in Alpine habitats during the reproductive season of the studied species. We found that rodents' T_b was positively correlated with elevation, the same for the two species inhabiting the entire elevation gradient. As expected, T_b in females was higher than in males, but this sex difference did not influence the elevation gradient. Air temperature influenced T_b only in one species, and habitat structure, as defined by plant richness and diversity and vegetation coverage, did not substantially affect T_b variation.

Rodents' T_b increased in our study with elevation, on average by 0.2 °C in mice and 0.3°C in voles every 200 m. In mountain habitats, especially during cold seasons, animals inhabiting high elevation are exposed to harsh environmental conditions. Low ambient temperatures and hypoxia (Storz et al. 2010) together can affect T_b regulation (Tattersall and Milsom 2009). For example, captive populations of deer mice (*Peromyscus maniculatus*) originating from highlands expressed higher oxygen consumption and T_b compared with captive populations from lowlands (Ivy and Scott 2017).

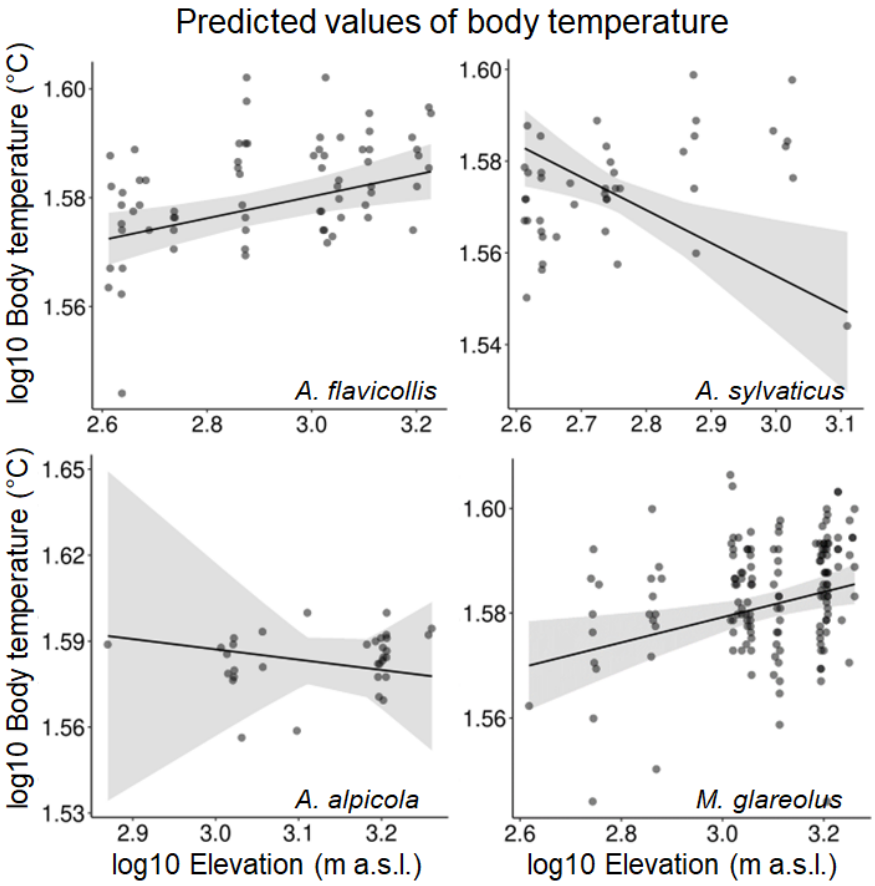

Figure 3. Predicted values of body temperature from regression models plotted against elevation, for *A. flavicollis*, *A. sylvaticus*, *A. alpicola* and *M. glareolus.*

In general, our results are consistent with these findings and also showed that wild rodents captured at higher elevations in the Alps maintained higher T_b during warm seasons compared with animals captured at lower elevations (figs. 1, 2). These results were consistent when considering species distributed across the complete elevation gradient studied here (*Apodemus flavicollis* and *Myodes glareolus*; fig. 3). The results were not significant in high-altitude species (*Apodemus alpicola*). In contrast, in species with lowland distribution (*Apodemus sylvaticus*), with very low densities at high altitudes (fig. 1), T_b was positively influenced by air temperature, and it was lower at higher elevations (fig. 3; table A4). The mechanisms behind these detected patterns are not clear. It may be hypothesised that plastic and adaptive responses in ventilatory performance (Ivy and Scott 2017)

and a-globin affinity for oxygen (Chappell and Snyder 1984; Sears et al. 2009), imperative for aerobic performance, are involved in differential responses among species. The cost for thermoregulation in homeothermic endotherms is high and increases with decreasing ambient temperature (Levy et al. 2011). Consequently, in species adapted to warm conditions, it would be energy efficient to reduce the body-environment temperature gradient (Gordon 2017). In our study, highland species did not reflect the T_b gradient according to air temperature, suggesting that they may be well adapted to low temperatures. However, we must be careful with this interpretation, as it could be influenced by the relatively weak environmental gradient during our study seasons, particularly for the highland species. We found that, on average, lowlands (12.3 °C at 400 m) were only 4.6 °C warmer than highlands (7.7 °C at 1,800 m). This difference in temperature along elevationis lower than expected (7.7 °C–9.1 °C for 1,400m of altitudinal range; Anslow and Shawn 2002) and may have made it difficult to detect the thermal environmental effects experienced by those species. Despite the weak air temperature gradient, the effect of air temperature on the T_b of the lowland species was evident, suggesting distinct physiological adaptation in *A. sylvaticus* compared with other *Apodemus* mice. Assessing T_b fluctuation in wild performing animals will provide detailed information about daily regulatory mechanisms and confirm patterns detected here on animals transferred to the common laboratory condition for measurements.

Our results showed that rodents from higher elevations expressed higher T_b than those from lower elevations. For most of the studied species, the effect was independent from variation in air temperature, habitat productivity, and body size or condition, suggesting that there are other mechanisms behind the detected pattern. It could be hypothesised that such a mechanism is related to mild tissue hypoxia and greater ventilation of individuals from higher elevations (Chappell and Snyder 1984). If true, it would suggest that even weak but chronic hypoxia can have a fitness effect in small endotherms, perhaps influencing their aerobic capacity performance. A comprehension of

the thermoregulation mechanisms of studied species could become even more critical considering climate change scenarios where the warmer temperatures in high altitudes are expected to become more frequent (Sears et al. 2009). Integrative studies on thermoregulation (i.e., behavioural adaptations, physiological mechanisms, and their selective benefits) and microhabitat use will help clarify how rodents adapted to extreme highland environments and shed light on the possibility for them to adapt to increasing air temperatures.

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Online Material

Table A1. Coordinates (longitude; latitude) of the twelve trapping location, the weather stations and the laboratories:

	Trapping locations		Weather stations		Laboratories	
1	7.62805	45.40565	7.57330	45.55680	7.52220	45.49770
2	7.61568	45.40899	7.48720	45.51350	7.31445	45.45137
3	7.59606	45.42822	7.61110	45.42000		
4	7.43559	45.42309	7.54100	45.40890		
5	7.54968	45.50748	7.43820	45.42670		
6	7.31445	45.45137	7.41150	45.43840		
7	7.39580	45.45295	7.31140	45.45280		
8	7.48709	45.51901	7.20910	45.44110		
9	7.47173	45.52610				
10	7.51484	45.55321				
11	7.21039	45.43669				
12	7.56948	45.55651				

Table A2. Descriptive statistics of phenotypic traits measured for *Apodemus flavicollis, A. sylvaticus, A. alpicola* and *Myodes glareolus* in the Gran Paradiso National Park divided into three altitudinal levels. Abbreviation: wt (body weight); hl (head length); hw (head width); bl (body length); BT (body temperature); SD (standard deviation).

A. flavicollis	< 1000 m a.s.l.		1000-1500 m a.s.l.		>1500 m a.s.l.		Female	Male
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	
wt (g)	30.0 (5.18)	21-43	30.5 (6.67)	19-43	26.1 (10.22)	17-40	30.5 (5.81)	31.6 (7.41)
hl (mm)	27.9 (2.81)	21.8-34	28.04 (2.70)	20.1-32	28.8 (2.88)	24-32.1	27.9 (2.86)	28.4 (2.60)
hw (mm)	15.5 (1.36)	10.2-17.9	15.6 (1.11)	13-17.9	15.3 (1.22)	13.5-17	15.3 (1.31)	15.5 (1.19)
bl (mm)	79.0 (7.69)	62-96	80.5 (6.45)	68-90	75.1 (10.92)	60-92	78.7 (6.8)	81 (8.2)
BT (°C)	37.6 (1.15)	35-40	38.3 (0.67)	37-40	38.7 (0.65)	37.5-39.5	38.3 (0.85)	37.96 (0.84)
A. sylvaticus								
wt (g)	29.8 (4.71)	22-43	28.5 (8.49)	18-38	-	-	27.7 (4.59)	30.8 (5.42)
hl (mm)	27.0 (2.38)	22.9-32	29 (3.29)	23-32	-	-	26.9 (2.11)	27.6 (2.63)
hw (mm)	15.4 (1.08)	13.2-17.9	15.2 (0.74)	14-16	-	-	15.4 (0.98)	15.3 (1.01)
bl (mm)	75.8 (7.35)	57-93	80.8 (9.78)	65-92	-	-	76.6 (6.04)	77.4 (8.78)
BT (°C)	37.3 (0.98)	35-39.7	37.9 (1.56)	35-39.6	-	-	37.8 (0.90)	37.3 (1.04)
A. alpicola								
wt (g)	-	-	28.8 (6.83)	17-40	29 (6.24)	18-40	28.5 (5.73)	29.7 (7.16)
hl (mm)	-	-	27.9 (2.04)	25-32	28.8 (1.44)	26-32	28.2 (1.82)	28.9 (1.65)
hw (mm)	-	-	15.8 (1.06)	14-17	15.5 (1.46)	13-18.9	15.4 (1.28)	15.8 (1.28)

bl (mm)	-	-	80.5 (8.94)	68-95	79.2 (8.12)	65-94	79 (7.45)	81 (9.42)
BT (°C)	-	-	38.3 (1.09)	36-39.8	38.5 (0.69)	37.1-39.8	38.5 (0.53)	38.2 (1.20)
M. glareolus								
wt (g)	25 (5.20)	14-36	26.8 (5.83)	14.5-35.5	30 (6.89)	13.5-38	27.9 (5.98)	27.1 (6.32)
hl (mm)	26.9 (4.09)	19.6-34	26.95 (2.33)	22-31.2	27.8 (2.99)	11.5-33	27.9 (3.13)	27.8 (2.52)
hw (mm)	14.5 (0.89)	12-16.2	14.92 (0.81)	13.8-16	15.1 (0.90)	13-17	14.9 (0.79)	14.8 (0.84)
bl (mm)	79.8 (7.52)	68-94	81.5 (9.29)	60-98	85.7 (10.12)	60-99	82.8 (8.27)	82.9 (9.84)
BT (°C)	37.7 (1.17)	35-39.8	38.3 (0.93)	36.2-40.4	38.7 (0.83)	36.9-40.1	38.5 (0.86)	38.1 (1.0)

NOTE. Abbreviations: wt (body weight); hl (head length); hw (head width); bl (body length); BT (body temperature); SD (standard deviation).

Table A3. Significance of the effect between body temperature and the tested variables in mixed-effects models.

	β (SE)	*z*	*p*
A. flavicollis	0.003 (0.002)	1.17	0.24
A. sylvaticus	0.001 (0.003)	0.33	0.74
M. glareolus	0.001 (0.002)	0.36	0.72
Season (1, 2)	-0.001 (0.002)	-0.42	0.67
Elevation	0.027 (0.005)	5.05	< **0.001**
T_{Emean}	0.023 (0.006)	3.93	< **0.001**
Sex (0,1)	0.004 (0.001)	3.94	< **0.001**
Plant richness	0.007 (0.009)	0.71	0.48
Vegetation coverage	-0.005 (0.009)	-0.53	0.59
Plant diversity	-0.002 (0.003)	-0.58	0.56
Exposure	-0.002 (0.003)	-0.57	0.57
BC	-0.007 (0.006)	-1.02	0.31
Head width	0.002 (0.020)	0.09	0.93

NOTE. The models included log_{10}-transformed variables (elevation; daily minimum air temperature, T_{Emean}; plant richness; plant diversity; vegetation coverage; exposure; head width) seasonality (1 for spring and 2 for summer) and body condition (BC) as continuous variables, sex (1 for female, 0 for male) and species (*A. flavicollis, M. glareolus, A. sylvaticus* and *A. alpicola*) as categorical factors. Bolded text highlights statistically-significant results.

Table A4. Single species models in which ten records with very low T_{Emean} (< 9.8 °C) were excluded. Species were analysed separately: (a) *A. flavicollis (*N = 69), (b) *A. sylvaticus (*N = 43), (c) *A. alpicola (*N = 33), (d) *M. glareolus (*N = 151). The effect of seasonality and the interaction effect between elevation and sex and elevation and T_{Emean} were excluded from these analyses due to the small sample size.

(a)

Apodemus flavicollis	β (SE)	*z*	*p*
Elevation	0.020 (0.006)	3.08	**0.003**
T_{Emean}	0.016 (0.026)	0.63	0.52
Sex (0,1)	0.006 (0.002)	2.53	**0.013**
Richness	0.0002 (0.018)	0.01	0.99
Plant diversity	0.001 (0.006)	0.22	0.82
Vegetation cover	0.007 (0.016)	0.46	0.64
Exposure	- 0.004 (0.004)	-0.91	0.36
BC	- 0.010 (0.013)	- 0.75	0.45
Head width	0.022 (0.030)	0.74	0.46

(b)

Apodemus sylvaticus	β (SE)	*z*	*p*
Elevation	- 0.071 (0.025)	- 2.85	**0.007**
T_{Emean}	0.233 (0.062)	3.75	**< 0.001**
Sex (0,1)	0.003 (0.003)	1.05	0.29
Richness	-0.006 (0.033)	-0.19	0.84
Plant diversity	- 0.019 (0.009)	- 2.13	0.040
Vegetation cover	- 0.044 (0.021)	- 2.08	0.044
Exposure	0.011 (0.005)	2.09	0.044
BC	-0.027 (0.026)	- 1.02	0.31
Head width	- 0.061 (0.059)	- 1.03	0.30

(c)

Apodemus alpicola	β (SE)	*z*	*p*
Elevation	-0.035 (0.107)	-0.33	0.74
T_{Emean}	0.031 (0.129)	0.24	0.81
Sex (0,1)	0.002 (0.004)	0.60	0.54
Richness	0.047 (0.051)	0.92	0.36
Plant diversity	0.021 (0.019)	1.11	0.27
Vegetation cover	- 0.054 (0.054)	- 1.01	0.32
Exposure	0.010 (0.022)	0.48	0.63
BC	- 0.046 (0.027)	- 1.70	0.10
Head width	- 0.026 (0.056)	- 0.46	0.64

(d)

Myodes glareolus	β (SE)	*z*	*p*
Elevation	0.024 (0.008)	2.75	**0.006**
T_{Emean}	0.003 (0.017)	1.18	0.85
Sex (0,1)	0.003 (0.001)	2.37	**0.018**
Richness	0.004 (0.012)	0.37	0.70
Plant diversity	- 0.007 (0.004)	- 1.70	0.091
Vegetation cover	0.007 (0.016)	0.48	0.63
Exposure	0.002 (0.004)	0.60	0.54
BC	- 0.011 (0.009)	- 1.26	0.21
Head width	- 0.010 (0.036)	-0.29	0.76
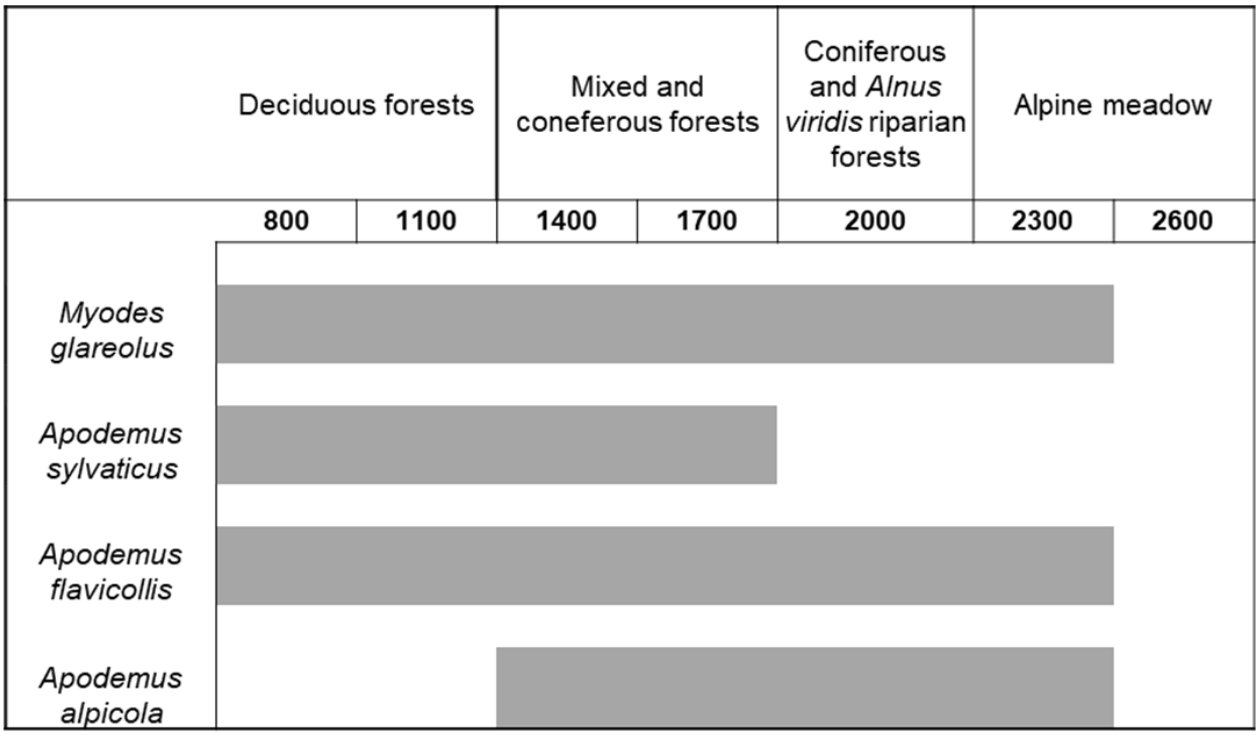
Figure A1. Altitudinal range distribution of the study species within the Gran Paradiso National Park.