



Environmental variation in the bioclimatic niche, hibernation patterns, and body size of Anatolian ground squirrels

Mutlu KART GÜR¹ · Tolga KANKILIÇ² · Hakan GÜR¹

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Abstract

Environmental variation in phenotypic traits offers key insights into how organisms adapt to diverse environmental conditions. In this study, we studied how diverse environmental conditions shape environmental variation in the bioclimatic niche, hibernation patterns, and body size of Anatolian ground squirrels (*Spermophilus xanthoprymnus*). Specifically, we used presence data from across the species' range, body temperature data from 51 free-living individuals in two natural populations located 880 km apart, and body size data from 167 individuals across 10 populations to explore environmental variation in bioclimatic niche, hibernation patterns, and body size across elevational and associated climatic gradients. Our results indicate that the bioclimatic niches of two deeply divergent mitochondrial (mt)DNA lineages (i.e., the western and eastern lineages) are not equivalent. However, this pattern appears to result from the underlying bioclimatic differences between the regions the western and eastern lineages inhabit. Anatolian ground squirrels from the eastern population, which inhabits a higher-elevation, colder, wetter, and more seasonally variable environment, exhibit longer hibernation periods, spend a higher proportion of this period in torpor bouts, and achieve deeper reductions in body temperature than conspecifics from the western population. Additionally, adult males exhibit shorter hibernation periods and spend a smaller proportion of this period in torpor bouts than the other age-sex classes. Anatolian ground squirrels from the eastern lineage, which inhabits areas at higher elevations with colder, wetter, and more seasonally variable environments, are morphologically larger than conspecifics from the western lineage, particularly among males. Overall, our results demonstrate that elevational and climatic gradients shape phenotypic variation in Anatolian ground squirrels through lineage-, population- and demographic-level responses. By integrating bioclimatic niche, hibernation patterns, and body size, this study highlights the importance of combining multiple trait dimensions to improve our understanding of eco-evolutionary divergence in hibernating mammals.

Keywords Anatolia · Ecological niche modelling · Physiological ecology · Environmental gradients · Niche overlap · Phenotypic variation · *Spermophilus xanthoprymnus*

Introduction

Environmental gradients provide valuable opportunities to study phenotypic variation. Populations of a species inhabiting different geographic regions typically experience diverse environmental conditions that drive adaptive differentiation (Bergmann 1847; Darwin 1859; Mayr 1956; Gould and Johnston 1972; McNab 2002). Although substantial research has examined environmental variation in niche, hibernation patterns, and body size of mammals across such gradients (Meiri and Dayan 2003; Dunbar and Brigham 2010; Mazel et al. 2017), these traits have rarely been studied in combination. To address this gap, in this study, we studied how diverse environmental conditions

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✉ Mutlu KART GÜR
mutlukartgur@gmail.com

¹ Anatolian Biogeography Research Laboratory, Kırşehir Ahi Evran University, Kırşehir, Türkiye

² Department of Biology, Sabire Yazıcı Faculty of Arts and Sciences, Aksaray University, Aksaray, Türkiye

shape phenotypic variation in a hibernating marmotine squirrel, focusing on the bioclimatic niche, hibernation patterns, and body size.

Anatolian ground squirrels, *Spermophilus xanthoprimum* (Bennett 1835), are group-living, diurnal, hibernating, and predominantly herbivorous, burrowing ground-dwelling rodents (Kart Gür and Gür 2010). They hibernate individually in underground burrows from late summer to late spring, with exact timing varying depending on geographic location, age, and sex (Gür and Kart Gür 2005; Kart Gür et al. 2009; Kart Gür and Gür 2015). Anatolian ground squirrels inhabit steppes and alpine vegetation at elevations ranging from approximately 800 m to 2,900 m above sea level. They are nearly endemic to Türkiye, primarily found in central and eastern (especially northeastern) Anatolia, with minor range extensions into western Armenia and northwestern Iran (Kryštufek and Vohralík 2005, 2012; Kart Gür and Gür 2010; Gür 2013, 2022). Phylogeographically, Anatolian ground squirrels are structured into two deeply divergent parapatric cytochrome b (cyt b) mitochondrial (mt) DNA lineages distributed along a west-east axis across central and eastern Anatolia (hereafter referred to as the western and eastern lineages, respectively), roughly divided by the Kızılırmak River (Fig. 1). These lineages consist of two and three sub-lineages in the western and eastern regions, respectively (Gündüz et al. 2007). Elevation increases from

central to eastern Anatolia (Fig. 1), resulting in substantial climatic variation, with environments becoming progressively colder, wetter, and more seasonally variable toward the east (Gür 2016). Consequently, Anatolian ground squirrels experience highly diverse environmental conditions throughout their range and are expected to exhibit phenotypic variation in response to these environmental differences. For instance, they follow a Bergmannian size pattern, with body size increasing as environmental temperature decreases (Gür 2010). These ecological and phylogeographic features collectively render Anatolian ground squirrels an excellent model system to study how elevational and associated climatic gradients shape environmental variation in bioclimatic niche, hibernation patterns, and body size.

Besides simultaneously studying bioclimatic niche, hibernation patterns, and body size, this study's significant contribution is examining a physiological trait (monitoring core body temperature during hibernation) in two geographically distinct populations under completely natural conditions. Although marmotine squirrels have been extensively studied in the context of hibernation, to our knowledge, outside of North America, no species of marmotine squirrel has been examined in terms of hibernation patterns in two distinct populations under natural conditions.

Specifically, we used presence data from across the species' range (72 and 98 presence records for the

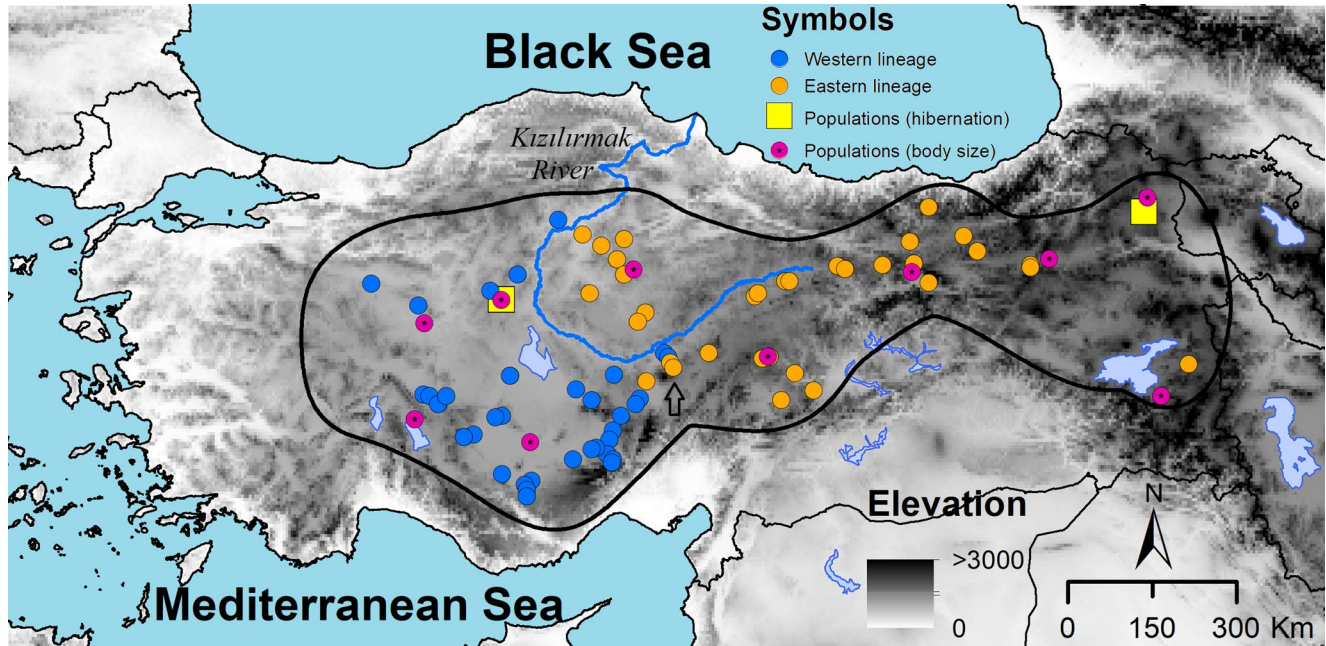


Fig. 1 The geographic distribution of Anatolian ground squirrels (*Spermophilus xanthoprimum*), as outlined by the bold black polygon, summarized from the “Monitoring Project for the Effects of Environmental Changes on Ground Squirrels.” Also shown are the distributions of the western and eastern lineages, based on 72 localities directly taken from Gündüz et al. (2007), which represent two deeply divergent parapatric cyt b mtDNA lineages distributed along a west–east axis across central

and eastern Anatolia. The locations of populations studied for hibernation patterns and body size are also indicated. Elevation data are shown in the background of the map. An open arrow on the map indicates the approximate location of a zone of secondary contact between the western and eastern lineages. For clarity, the Kızılırmak River is labeled. The map spans from 25° to 46° E longitude and 35° to 43° N latitude. See inset legend for symbol descriptions

western and eastern lineages, respectively), body temperature data from 51 free-living individuals in two natural populations located 880 km apart (one population from each lineage, representing near-extremes of the species' environmental range), and body size data from 167 individuals across 10 populations (four and six populations from the western and eastern lineages, respectively, broadly representing the species' environmental range) to explore environmental variation in bioclimatic niche, hibernation patterns, and body size across elevational and climatic gradients. Thus, as environmental conditions become progressively higher in elevation, colder, wetter, and more seasonally variable from central to eastern Anatolia, we had the opportunity to examine how the western and eastern lineages and the populations from both lineages respond to this environmental gradient. We hypothesized that environmental variation in bioclimatic niche, hibernation patterns, and body size would show congruent patterns, reflecting adaptive responses to environmental conditions.

Methods

Ethics statements

All procedures involving animals in this study followed the ethical standards outlined in the *Guidelines for the Capture, Handling, and Care of Mammals* approved by the American Society of Mammalogists (Animal Care and Use Committee 1998), as well as the *Guide for the Care and Use of Laboratory Animals* (Institute for Laboratory Animal Research [ILAR] 1996).

Bioclimatic niche

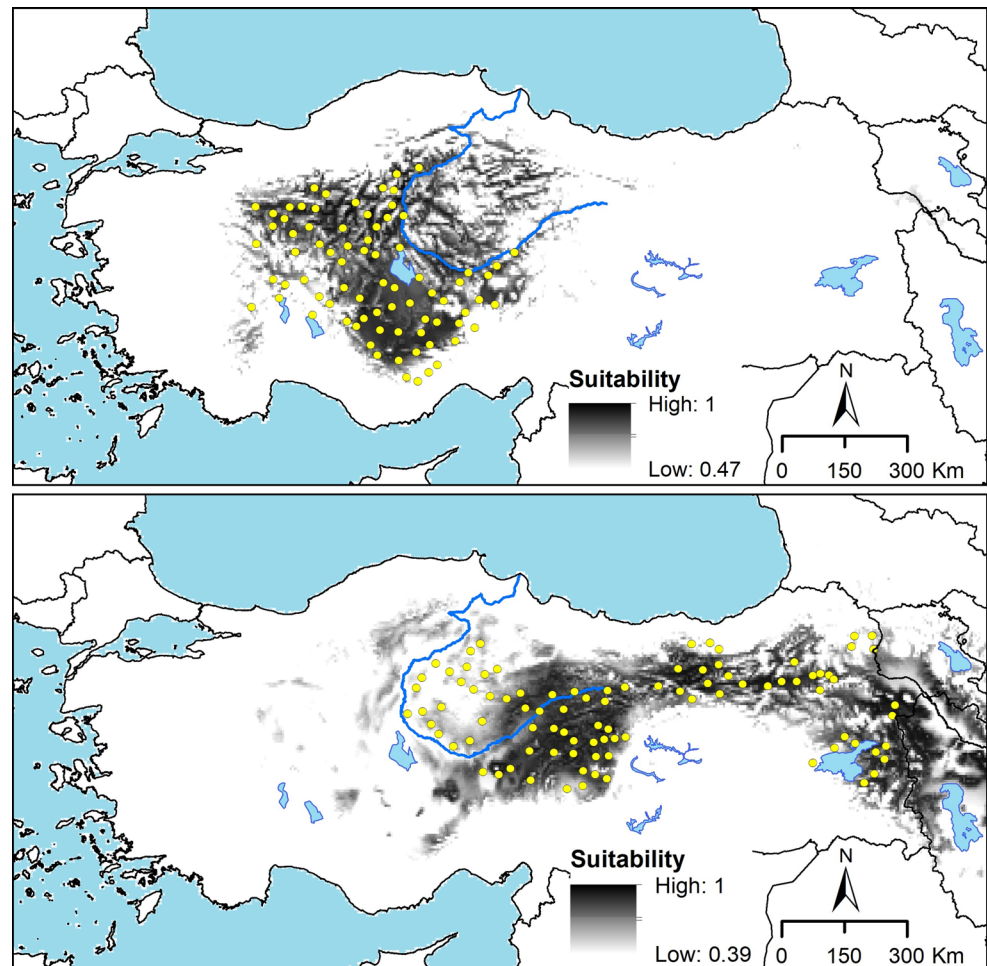
For Anatolian ground squirrels (*Spermophilus xanthopyrmus*), presence data (538 records) spanning the period 1990s–2018 and covering the species' range were obtained from the Monitoring Project for the Effects of Environmental Changes on Ground Squirrels. This project also collects presence records of ground squirrels in Anatolia, primarily through field studies conducted throughout the active season, especially in spring (Gür 2022). To minimize the effects of spatial sampling biases (Boria et al. 2014), the presence records were spatially filtered by reducing multiple records into a single record within distances of 10 km, 15 km, and 20 km in areas of high, medium, and low environmental heterogeneity, respectively, as implemented in the software SDMtoolbox v2.6 (Brown et al. 2017). This spatial filtering resulted in 170 records used for ecological niche modelling and niche overlap analyses.

To explore environmental variation in the bioclimatic niche, the geographic distribution of Anatolian ground squirrels was first divided into two parts (the western and eastern lineages) based on the known ranges of two deeply divergent parapatric cyt b mtDNA lineages (i.e., 72 localities in Gündüz et al. 2007) distributed along a west-east axis across central and eastern Anatolia (Fig. 1). This division was achieved by generating Voronoi polygons from the input localities and grouping each polygon according to lineage relationships. Subsequently, 170 records were assigned to the western and eastern lineages (78 and 92 records, respectively), also taking into account the Kızılırmak River as a geographic reference, as implemented in the software SDMtoolbox v2.6 (Brown et al. 2017) (Fig. 2).

Bioclimatic data, originally at a spatial resolution of 30 arc-seconds, were downloaded from the CHELSA database for present (1979–2013) conditions (Karger et al. 2017a, b) and subsequently resampled to a spatial resolution of 2.5 arc-minutes. These data include 19 bioclimatic variables derived from monthly temperature and mean precipitation values. Based on current knowledge about the ecology of ground squirrels and long-term niche modelling analyses conducted as part of the Monitoring Project for the Effects of Environmental Changes on Ground Squirrels (Gür 2010, 2013; Kart Gür and Gür 2010; Gür and Kart Gür 2012; Gür et al. 2018; Gür 2022), a subset of eight bioclimatic variables was selected: annual mean temperature and precipitation (BIO1 and 12), temperature and precipitation seasonality (BIO4=temperature seasonality, the standard deviation of monthly mean temperatures from the annual mean; it reflects the amount of monthly temperature variation over the year and BIO15=precipitation seasonality, the coefficient of variation of monthly precipitation totals; it reflects the amount of monthly precipitation variation over the year), and mean temperature and precipitation of the coldest and warmest quarters (BIO10, 11, 18, and 19) (Table 1). All selected variables were masked to include only Anatolia and its surrounding regions (study area defined as 25° to 46° E and 35° to 43° N; Gür 2013) (Fig. 1).

To model the bioclimatic niches (i.e., the Grinnellian niches focusing on a species' scenopoetic requirements or bioclimatic suitability) of the western and eastern lineages, the software MaxEnt v3.4.4 (Phillips et al. 2017) was used. MaxEnt is a machine-learning algorithm that relies on presence-only data and implements a presence-background modeling approach by contrasting environmental conditions at presence data with randomly sampled background data (Peterson et al. 2011; Phillips et al. 2017). It generally outperforms alternative modeling approaches (Elith et al. 2006) and has previously demonstrated comparable performance to a complex ensemble model for this species (Gür 2022). The optimal model settings were identified using the

Fig. 2 Areas of high bioclimatic suitability for the western (above) and eastern (below) lineages of Anatolian ground squirrels (*Spermophilus xanthoprimum*), identified as regions exceeding the ‘10th percentile training presence’ thresholds (0.39 for the western lineage and 0.47 for the eastern lineage). Yellow circles indicate 78 presence records for the western lineage (above) and 92 presence records for the eastern lineage (below)



software WALLACE v2.2.0, an open-source GUI that facilitates access to modern R-based workflows (Kass et al. 2018; for further details, see Muscarella et al. 2014; for Turkish tutorial, see Gür 2019), following the same analytical workflow used in our previous studies (Gür 2022; Dumlupınar et al. 2023). A minimum convex polygon around all presence records from both lineages (170 records), with a 2-degree buffer, was used to define the background extent. All pixels within this extent were used as background data (55,241 pixels at a spatial resolution of 2.5 arc-minutes). To regulate model complexity, 25 candidate models were tested by combining five feature class sets [Linear (L), Linear and Quadratic (LQ), Hinge (H), Linear, Quadratic, and Hinge (LQH), and Linear, Quadratic, Hinge, and Product (LQHP)] with five regularization multiplier values (ranging from 1 to 5, incremented by 1). Model evaluation statistics were calculated using spatial checkerboard-2 cross-validation (block partitioning, $k=4$; aggregation factor=4). The optimal model settings were selected based on the highest Continuous Boyce Index (CBI), with additional support from threshold-independent (AUC_{TEST} and AUC_{DIFF}) and threshold-dependent (OR_{MIN} , ‘Minimum Training Presence’

omission rate and OR_{10} , 10% training omission rate) evaluation statistics, averaged across iterations. Once the optimal model settings were identified, final models were trained separately for the western and eastern lineages, using the full, unpartitioned dataset (78 and 92 records, respectively), along with 55,241 background pixels, for eight bioclimatic variables. For these final models, significance were evaluated through a partial ROC analysis (Peterson et al. 2008), as implemented in the software NicheToolBox, ntbox v0.7.2 (Osorio-Olvera et al. 2020). Additionally, the univariate response curves were examined to assess their biological plausibility, and all appeared to be biologically reasonable.

To assess differences in the bioclimatic niches of the western and eastern lineages, two quantitative tests of niche overlap, namely the niche equivalency test and the niche similarity test (Warren et al. 2008; Broennimann et al. 2012), were conducted, as implemented in the software WALLACE v2.2.0 (Kass et al. 2018; for further details, see Broennimann et al. 2012) and the R package ecospat v4.1.2 (Di Cola et al. 2017). The niche equivalency test evaluates whether the niches of species or populations are statistically equivalent, whereas the niche similarity test provides further insights, allowing

Table 1 Contributions of bioclimatic variables, evaluation statistics (mean±SD), and model settings for the final ecological niche models, and descriptive statistics (median and interquartile range, IQR) for bioclimatic variables and elevation for the western ($n=78$) and eastern ($n=92$) lineages of Anatolian ground squirrels (*Spermophilus xanthopyrmnus*). P values were adjusted for false discovery rate. Asterisks indicate significance levels (* $P<0.05$, ** $P<0.001$). BIO1=annual mean temperature. BIO4=temperature seasonality (the standard deviation of monthly mean temperatures from the annual mean; it reflects the amount of monthly temperature variation over the year). BIO10=mean temperature of the warmest quarter. BIO11=mean temperature of the coldest quarter. BIO12=annual precipitation. BIO15=precipitation seasonality (the coefficient of variation of monthly precipitation totals; it reflects the amount of monthly precipitation variation over the year). BIO18=precipitation of the warmest quarter. BIO19=precipitation of the coldest quarter

Variables/statistics/parameters	Contributions/statistics/settings		Descriptive statistics (median and IQR)	
	Western lineage	Eastern lineage	Western lineage	Eastern lineage
BIO1 (°Cx10)**	0.3736/1.1267	0.4108/0.8564	12.1 (10.7–12.7)	8.4 (7.0–9.8)
BIO4 (standard deviationx100)**	0.3167/1.1012	0.3193/0.8578	8.1 (7.8–8.3)	8.3 (8.1–8.8)
BIO10 (°Cx10)**	0.2816/1.1267	0.3439/0.8677	23.4 (22.0–24.2)	20.2 (18.8–21.5)
BIO11 (°Cx10)**	0.5157/1.0743	0.4944/0.8064	1.3 (0.2–2.0)	−3.3 (−4.5–1.1)
BIO12 (mm)**	0.5947/1.0502	0.3031/0.8602	365 (339–410)	430 (385–471)
BIO15 (coefficient of variation)*	0.3069/1.1158	0.3547/0.8603	44 (39–48)	47 (42–51)
BIO18 (mm)	0.3603/1.1210	0.2297/0.8326	26 (17–35)	28 (21–41)
BIO19 (mm)*	0.3423/1.1104	0.4188/0.8616	120 (107–144)	113 (99–137)
Elevation (m)**			1034 (959–1192)	1586 (1300–1784)
CBI	0.893±0.048	0.851±0.091		
AUC _{TEST}	0.909±0.023	0.861±0.028		
AUC _{DIFF}	0.016±0.023	0.028±0.017		
OR _{MIN}	0.037±0.052	0.022±0.025		
OR ₁₀	0.100±0.093	0.107±0.053		
Feature class	L, Q, and H	L, Q, H, and P		
Regularization multiplier	4	3		

Note that elevation was not included in ecological niche modelling

Variables in **bold** indicate the strongest contributors to the final models, as determined by the jackknife test

CBI=Continuous Boyce Index. AUC_{TEST} and AUC_{DIFF} = threshold-independent evaluation statistics. OR_{MIN}, ‘Minimum Training Presence’ omission rate and OR₁₀, 10% training omission rate=threshold-dependent evaluation statistics

Feature classes: L=Linear, Q=Quadratic, H=Hinge, P=Product

detection of niche differences that cannot be attributed solely to environmental differences between the regions species or populations (in this case, the western and eastern lineages) inhabit. These tests were performed in environmental space rather than in geographic space. This approach was preferred because evaluating niche overlap based on geographic projections of ecological niche models can be problematic: the degree of overlap may vary depending on the extent and distribution of environmental gradients across the study area and may also be influenced by statistical artifacts introduced during model fitting (Broennimann et al. 2012). Niche overlap analyses were performed following a three-step framework: (1) Principal Component Analysis (PCA) was used to reduce the dimensionality of eight bioclimatic variables, calibrated using 10,000 background pixels drawn from the 2-degree buffered minimum convex polygons surrounding the presence records of each lineage (environmental ordination); (2) the smoothed densities of the presence records and background environments were generated for each lineage across a 100×100 grid of the environmental space defined by the first two PCA axes, using a kernel density smoothing approach (occurrence density grid); and (3) Schoener’s D metric was calculated to quantify niche overlap between the western and eastern lineages,

with the niche equivalency and similarity tests conducted using 1000 randomized pseudoreplicates corrected for environmental availability differences (niche overlap).

In addition to niche overlap analyses, a separate PCA was performed to visualize differences in the bioclimatic niches of the western and eastern lineages. The analysis was based on a correlation matrix derived from the data for 170 records and eight bioclimatic variables, along with elevation, using the software PAST v5.1 (Hammer and Harper 2001). Elevation data (Jarvis et al. 2008) were incorporated to assess the contribution of elevation to bioclimatic differences between both lineages. This visualization highlights how the western and eastern lineages segregate along major environmental gradients and situates the populations studied for hibernation patterns and body size within the environmental space. Differences in environmental variables between both lineages were assessed using a Mann-Whitney U test, implemented in IBM SPSS Statistics.

Hibernation patterns

To explore environmental variation in the hibernation patterns of Anatolian ground squirrels, body temperature (Tb) data were collected from 51 free-living individuals in two

geographically distinct populations. The first population (23 individuals) belongs to the western lineage (39.48 N, 32.85 E, 1200 m, Ankara province), and the data from this population have been previously published (Kart Gür et al. 2009; Kart Gür and Gür 2015). The second population (28 individuals) represents the eastern lineage (40.55 N, 43.10 E, 1770 m, Kars province), and the data from this population were collected specifically for this study and have not been published previously. These populations (hereafter referred to as the western and eastern populations) are located 880 km apart from each other (Fig. 1).

Field studies were conducted during 2005–2007 for the western population (covering two hibernation seasons) and during 2013–2014 for the eastern population (covering one hibernation season). Although Tb data for the western and eastern populations were collected in different years, this does not compromise comparability, as both populations differ substantially in elevation and climate, representing near-extremes within the species' range. Thus, between-population differences are expected to exceed within-population differences. Moreover, year-to-year variation within each population was considered limited and did not obscure population-specific patterns, as previously demonstrated for the western population (Kart Gür and Gür 2015).

Anatolian ground squirrels were trapped using live traps (Tomahawk Live Trap Co., Tomahawk, WI, USA) at irregular intervals throughout the active season. At initial capture, each individual was permanently marked with numbered metal ear tags (National Band and Tag Co., Newport, KY, USA). At each capture, date, tag number, age, sex, body mass (± 5 g, Pesola spring scale; Pesola AG, Rebmattli, Baar, Switzerland), and reproductive status were recorded. Individuals were classified as juvenile if captured during the active season of their birth year and as adult after their first hibernation (Gür and Kart Gür 2005; Kart Gür and Gür 2010). At initial capture, juveniles were distinguished from adults by size and mass. Near the end of the active season, temperature data loggers were surgically implanted into the peritoneal cavity of 37 individuals (eight adult males, 13 adult females, seven juvenile males, and nine juvenile females) from the western population and 32 individuals (eight adult males, eight adult females, eight juvenile males, and eight juvenile females) from the eastern population to measure core Tb. The devices used were either ThermoChron iButtons (DS1922L, ~3 g, range -40 to 85 °C, resolution 0.0625 or 0.5 °C; Maxim Integrated Products, Inc., Sunnyvale, CA, USA) or StowAway Tidbits (customized temperature data logger, 8.7 g, range -4 to 44 °C, resolution 0.16 °C; Onset Computer Corporation, Bourne, MA, USA). Both types of devices were used in individuals from both the western and eastern populations. They were programmed to record Tb at intervals of 15 min (StowAway Tidbits) or

50 min (with a resolution of 0.5 °C, ThermoChron iButtons). At the beginning of the subsequent active season, the loggers were surgically removed from 23 surviving individuals (three adult males, nine adult females, four juvenile males, and seven juvenile females) in the western population and 30 surviving individuals (eight adult males, seven adult females, eight juvenile males, and seven juvenile females) in the eastern population. However, complete Tb data were not recovered from two individuals (one adult female and one juvenile male) in the eastern population due to device malfunction or data loss. Throughout the hibernation season, soil temperature (Tsoil) was monitored at 1 m depth (the expected hibernacula depth; Karabağ 1953; Kart Gür et al. 2009; Kart Gür and Gür 2015) using a temperature logger (DS1922L; for specifications, see above). The preparation of the loggers and the surgical procedures were carried out following the protocols described in Kart Gür et al. (2009) and Kart Gür and Gür (2015). In line with ethical standards, the total weight of the wax-coated loggers remained within acceptable limits, corresponding to approximately 3–5% of the animals' body mass, as previously discussed in detail in these studies.

Tb data of 51 Anatolian ground squirrels from the western and eastern populations were analyzed for hibernation parameters (Table 2). Hibernation was defined as the period extending from the initiation of the first multiday torpor bout to the termination of the last such bout, during which individuals remained continuously underground (Kart Gür et al. 2009; Ruf and Geiser 2014; Kart Gür and Gür 2015). Torpor bouts were defined as periods extending from the first point when Tb was < 30 °C to the first point when Tb was > 30 °C, whereas interbout arousals were defined as periods extending from the first point when Tb was > 30 °C to the first point when Tb was < 30 °C (Young 1990; Michener 1992; Ruf and Arnold 2000; Zervanos and Salsbury 2003; Buck et al. 2008; Kart Gür et al. 2009; Lee et al. 2009; Healy et al. 2012; Kart Gür and Gür 2015). Multiday torpor bouts lasted longer than 24 h, whereas short torpor bouts lasted less than 24 h (Kart Gür et al. 2009; Ruf and Geiser 2014; Kart Gür and Gür 2015).

Variation in any hibernation parameter of interest between the western and eastern populations, as well as among age-sex classes, was evaluated using a two-way ANOVA (Sokal and Rohlf 1995), implemented in IBM SPSS Statistics, according to the following statistical design:

$$\text{Hibernation parameter} = \text{Intercept} + \text{Population} + \text{Age-Sex class} + \text{Population} * \text{Age-Sex class}$$

Pairwise post-hoc comparisons were conducted using Tukey's Honestly Significant Difference (HSD) test to assess differences among all combinations of age-sex classes within and between populations, while controlling for Type I error across multiple comparisons.

Table 2 Summary of the hibernation patterns of Anatolian ground squirrels (*Spermophilus xanthopyrmnus*) by population and age-sex class. Descriptive statistics were presented as mean±se and range. *P* values were adjusted for false discovery rate. Asterisks indicate significance levels (**P*<0.05, ***P*<0.01, ****P*<0.001). Please note that mean duration of torpor bouts (days) and mean duration of interbout arousals (days) are based on mean value throughout hibernation for each individual

Parameter	Population	Age-sex classes				F-statistics
		Adult males	Adult females	Juvenile males	Juvenile females	
Sample size (n)	Western	3	9	4	7	
	Eastern	8	6	7	7	
Beginning of hibernation (date)	Western	31 Aug±6.66 (22 Aug–13 Sep)	15 Aug±4.89 (04 Aug–18 Sep)	10 Sep±2.87 (03–17 Sep)	09 Sep±1.84 (02–16 Sep)	Pop: F(1,43)=123.72*** Age-sex: F(3,43)=17.76***
	Eastern	4 Aug±2.71 (19 Jul–10 Aug)	27 Jul±2.31 (21 Jul–04 Aug)	9 Aug±0.51 (07–11 Aug)	11 Aug±1.16 (07–15 Aug)	Interaction: F(3,43)=1.28
End of hibernation (date)	Western	14 Feb±3.48 (08–20 Feb)	10 Mar±2.20 (02–22 Mar)	09 Mar±4.82 (02–23 Mar)	27 Mar±3.46 (16 Mar–09 Apr)	Pop: F(1,43)=83.25*** Age-sex: F(3,43)=39.65***
	Eastern	10 Mar±0.80 (07–13 Mar)	27 Mar±2.43 (19 Mar–03 Apr)	7 Apr±1.75 (29 Mar–11 Apr)	03 Apr±3.62 (19 Mar–11 Apr)	Interaction: F(3,43)=5.62**
Spring body mass (g)	Western	252±12 (235–275)	182±6 (145–205)	175±12 (160–210)	156±7 (130–190)	Pop: F(1,43)=1.62 Age-sex: F(3,43)=64.11***
	Eastern	286±7 (265–320)	190±13 (165–245)	169±4 (155–185)	151±6 (135–175)	Interaction: F(3,43)=2.23
Total duration of hibernation (days)	Western	167.50±3.68 (160.17–171.70)	207.17±5.29 (168.58–222.57)	180.22±6.31 (166.15–195.64)	198.87±3.04 (185.00–209.14)	Pop: F(1,43)=245.45*** Age-sex: F(3,43)=20.33***
	Eastern	218.16±2.79 (211.46–234.21)	242.86±3.10 (229.92–252.80)	241.04±1.61 (233.14–244.96)	234.35±2.81 (223.00–242.02)	Interaction: F(3,43)=4.58*
Mean duration of torpor bouts (days)	Western	6.33±0.25 (5.83–6.59)	7.74±0.17 (6.72–8.29)	8.64±0.35 (7.96–9.50)	8.02±0.33 (7.24–9.74)	Pop: F(1,43)=25.66*** Age-sex: F(3,43)=10.62***
	Eastern	8.18±0.19 (7.67–9.10)	8.51±0.24 (7.91–9.40)	8.81±0.13 (8.30–9.22)	8.83±0.23 (8.03–9.56)	Interaction: F(3,43)=3.14*
Mean duration of interbout arousals (days)	Western	1.14±0.05 (1.08–1.24)	0.92±0.02 (0.86–0.99)	0.91±0.06 (0.83–1.09)	0.77±0.05 (0.67–1.05)	Pop: F(1,43)=59.28*** Age-sex: F(3,43)=36.49***
	Eastern	0.94±0.02 (0.82–0.99)	0.77±0.02 (0.73–0.82)	0.71±0.01 (0.66–0.75)	0.66±0.01 (0.63–0.68)	Interaction: F(3,43)=0.92
Duration of the longest torpor bout (days)	Western	14.04±1.39 (11.88–16.63)	17.59±0.59 (14.91–20.21)	18.84±0.33 (18.02–19.61)	18.07±0.74 (16.33–22.04)	Pop: F(1,43)=68.54*** Age-sex: F(3,43)=5.03**
	Eastern	20.83±0.88 (16.89–25.04)	21.27±0.38 (19.68–22.27)	21.76±0.50 (19.21–23.42)	21.56±0.40 (20.46–23.16)	Interaction: F(3,43)=2.41
Number of torpor bouts	Western	22.67±1.20 (21–25)	24.11±0.72 (20–28)	19.00±0.41 (18–20)	22.71±0.81 (20–26)	Pop: F(1,43)=31.78*** Age-sex: F(3,43)=5.95**
	Eastern	23.88±0.61 (22–27)	26.33±0.80 (24–29)	25.43±0.37 (24–27)	24.86±0.63 (23–28)	Interaction: F(3,43)=4.33*
Total duration of torpor bouts (days)	Western	142.90±2.32 (138.33–145.87)	186.06±4.96 (149.79–199.13)	164.04±6.98 (147.68–180.54)	182.02±3.37 (168.93–194.76)	Pop: F(1,43)=276.42*** Age-sex: F(3,43)=27.37***
	Eastern	196.48±2.30 (190.38–209.71)	223.39±2.86 (210.79–231.68)	223.67±1.50 (215.77–226.92)	218.59±2.88 (207.25–226.01)	Interaction: F(3,43)=4.34*
Total duration of interbout arousals (days)	Western	24.59±1.38 (21.84–26.11)	21.12±0.61 (18.78–23.44)	16.19±0.77 (15.09–18.47)	16.86±0.96 (12.74–21.07)	Pop: F(1,43)=4.57* Age-sex: F(3,43)=34.80***
	Eastern	21.68±0.75 (18.84–24.50)	19.47±0.52 (17.42–21.12)	17.37±0.33 (16.25–18.83)	15.76±0.33 (14.88–17.14)	Interaction: F(3,43)=2.31
Total duration of torpor bouts as % of hibernation	Western	85.34±0.52 (84.70–86.36)	89.79±0.26 (88.85–90.99)	90.95±0.74 (88.88–92.28)	91.50±0.52 (89.21–93.86)	Pop: F(1,43)=108.76*** Age-sex: F(3,43)=59.65***
	Eastern	90.07±0.27 (89.06–91.09)	91.98±0.19 (91.65–92.79)	92.79±0.12 (92.28–93.24)	93.27±0.17 (92.59–93.77)	Interaction: F(3,43)=6.53**
Lowest minimum steady-state Tb (°C)	Western	7.10±0.51 (6.59–8.11)	5.42±0.42 (3.61–7.62)	4.63±0.40 (3.67–5.54)	3.66±0.58 (1.67–6.19)	Pop: F(1,43)=98.23*** Age-sex: F(3,43)=5.40**
	Eastern	1.69±0.62 (–1.45–3.50)	1.62±0.43 (0.51–3.22)	1.96±0.37 (1.03–3.50)	0.96±0.27 (0.04–2.01)	Interaction: F(3,43)=2.67

Body size

To explore environmental variation in the body size of Anatolian ground squirrels, the skulls of 167 adults (89 females and 78 males) across 10 populations (Fig. 1), covering most of the species' range, were analyzed. These specimens were previously examined in Gür (2010) as part of a phylogenetic comparative analysis of geographic variation in body size in relation to environmental variables and are reanalyzed here to assess variation in body size between western and eastern lineages. Of these populations, four (52 adults: 32 females and 20 males) belong to the western lineage and six (115 adults: 57 females and 58 males) to the eastern lineage.

Body size (here referring to skull size) was estimated using geometric morphometric analysis, which was preferred over traditional morphometric analysis employed in Gür (2010), as it enables a more effective separation of size and shape components (Bookstein 1991; Dryden and Mardia 1998). Accordingly, first, 12 two-dimensional landmarks, assumed to be homologous among all individuals analyzed, were digitized on the right side of the ventral view of the skulls, using the software tpsDig (Rohlf 2010). Then, skull size was estimated by the centroid size of landmark configurations, superimposed by Procrustes analysis (Dryden and Mardia 1998), using the software MorphoJ (Klingenberg 2011). Variation in skull size due to digitizing error was very low when a subsample of individuals (i.e., 30 randomly selected skulls) was digitized again and therefore skull size was estimated twice for these individuals.

Variation in body size between the western and eastern lineages, as well as among populations and between sexes, was evaluated using a generalized linear model (GLM; McCullagh and Nelder 1989) with a normal probability distribution and identity link function, implemented in IBM SPSS Statistics, according to the following statistical design:

$$\text{Body size} = \text{Intercept} + \text{Lineage} + \text{Sex} + \text{Lineage} * \text{Sex} + \text{Population}(\text{Lineage}) + \text{Population} * \text{Sex}(\text{Lineage})$$

Results

Bioclimatic niche

The final models for the western and eastern lineages of Anatolian ground squirrels (*Spermophilus xanthoprymus*) were developed using the optimal settings reported in Table 1, which were selected based on model evaluation statistics collectively indicating strong performance, with high discriminatory power and minimal overfitting. These models were statistically significant (i.e., the difference between

the AUC from model predictions and the AUC from random predictions was greater than zero, $P < 0.001$ for each model).

Areas of high bioclimatic suitability (i.e., areas with suitability values above the '10 percentile training presence' threshold) were predicted separately for each lineage, mainly in the western and eastern portions of the species' range, corresponding to the geographic distributions of the western and eastern lineages, respectively (Fig. 2), indicating spatial concordance between the combined lineage ranges and the overall distribution of Anatolian ground squirrels (Figs. 1 and 2). High suitability areas for both lineages were predicted along the course of the Kızılırmak River (Fig. 2); however, actual overlap was observed only south of the river, in terrain devoid of the river yet still bioclimatically suitable for each lineage, a pattern consistent with a zone of secondary contact (Fig. 1). In contrast, the bowl-shaped interior enclosed by the Kızılırmak River, also highly suitable for the western lineage, was inhabited exclusively by the eastern lineage. Taken together, these patterns indicated that the Kızılırmak River acted as a strong dispersal barrier, whereas farther south, beyond the river's influence, overlap remained limited and highly localized (Figs. 1 and 2). Annual mean precipitation (BIO12) dominated the western-lineage model, whereas mean temperature of the coldest quarter (winter temperature, BIO11) dominated the eastern-lineage model (Table 1); notably, these same variables also distinguished the lineages in the PCA (Fig. 3). As noted above, areas of high bioclimatic suitability for the western and eastern lineages were largely confined to the immediate vicinity of the Kızılırmak River and overlapped only marginally elsewhere (Fig. 2), suggesting that the bioclimatic niches of both lineages were not equivalent. This inference was supported by the niche equivalency test ($D = 0.212$, $P < 0.001$). The niche similarity test further showed that the western lineage shared most of its bioclimatic niche with the eastern lineage (unfilling, unique fraction = 0.031), whereas the eastern lineage shared only about half of its bioclimatic niche with the western lineage (unfilling, unique fraction = 0.556). The univariate response curves, PCA results, and descriptive statistics consistently indicated that the eastern lineage inhabits areas at higher elevations with colder, wetter, and more seasonally variable environments than the western lineage (Table 1; Fig. 3). Nevertheless, the niche differences suggested by all these results can be explained solely by bioclimatic differences between the regions the western and eastern lineages inhabit ($D = 0.185$, $P = 0.068$ for the western lineage vs. the eastern background and $P = 0.087$ for the eastern lineage vs. the western background). Consequently, we find no evidence of intrinsic bioclimatic niche divergence between both lineages.

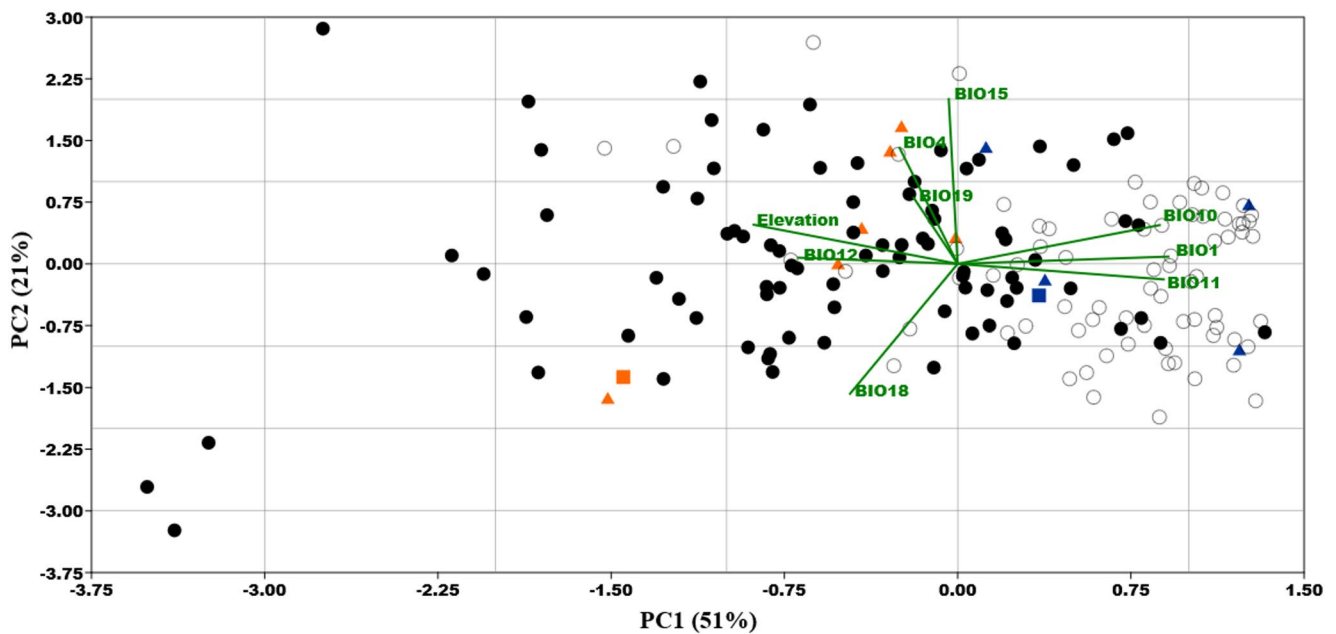


Fig. 3 Environmental space of Anatolian ground squirrels (*Spermophilus xanthoprymnus*) based on principal component analysis (PCA) of eight bioclimatic variables and elevation for 170 presence records (72 from the western lineage and 98 from the eastern lineage). The PCA was conducted to visualize variation in environmental conditions across the species' range and to assess the degree of environmental differentiation between western and eastern lineages. Open and filled black circles represent western and eastern records, respectively. Also plotted are the populations studied for hibernation patterns (filled squares: blue=western, orange=eastern) and body size (filled trian-

gles: blue=western, orange=eastern), showing their relative positions within the environmental space defined by the first two PCA axes. The biplot also includes vectors representing the correlation of environmental variables with the first two axes. BIO1=annual mean temperature. BIO4=temperature seasonality. BIO10=mean temperature of the warmest quarter. BIO11=mean temperature of the coldest quarter. BIO12=annual precipitation. BIO15=precipitation seasonality. BIO18=precipitation of the warmest quarter. BIO19=precipitation of the coldest quarter (BIO19)

Hibernation patterns

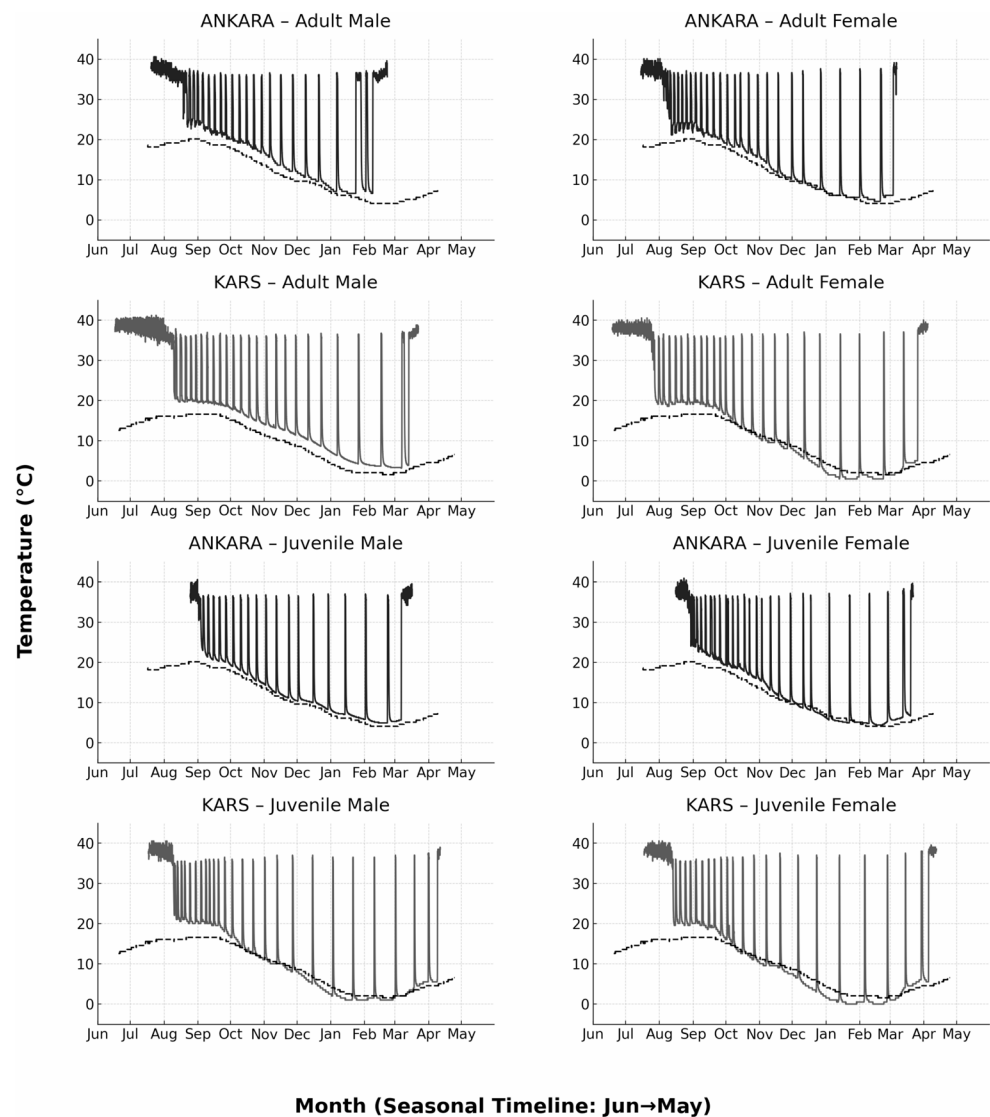
The PCA results revealed that the western and eastern populations, in which environmental variation in hibernation patterns was examined, were largely differentiated along an environmental gradient (PC1) primarily defined by elevation, temperature variables, and annual precipitation (Fig. 3). The ANOVA results showed significant main effects of both population and age-sex class on all hibernation parameters, except for spring body mass, which showed no significant effect of population (Table 2). The eastern population consistently entered hibernation earlier, emerged later, and consequently exhibited a longer hibernation period than the western population. Additionally, it experienced longer durations in torpor bouts and shorter durations in interbout arousals, spent a higher proportion of the hibernation period in torpor bouts, and reached lower minimum Tbs (Table 2), closely aligned with the lower ambient (soil) temperatures (Fig. 4). Remarkably, in one adult male from this population, we recorded sub-zero intraperitoneal Tbs during 5 out of 23 torpor bouts, lasting a total of 47 days and 7 h. This observation suggests that, although rare, episodes of supercooling may indeed occur. Post-hoc comparisons

using Tukey's HSD test showed that adult males exhibited the greatest number of statistically significant differences when compared to other age-sex classes. Specifically, they emerged earlier and at a greater body mass, exhibited shorter hibernation periods, experienced shorter durations in torpor bouts and longer durations in interbout arousals, spent a smaller proportion of the hibernation period in torpor bouts (Table 2; Fig. 4). However, significant interaction effects of population and age-sex class were detected for a subset of hibernation parameters (Table 2), indicating that the physiological responses of both populations to environmental conditions are not consistent across age-sex classes and that such demographic variation is specific to certain aspects of hibernation.

Body size

The PCA results revealed that the populations, for which environmental variation in body size was examined, were differentiated along two environmental gradients: the first (PC1) primarily defined by elevation, temperature variables, and annual precipitation, and the second (PC2) primarily by summer precipitation and seasonality variables (Fig. 3). The GLM results showed significant main effects

Fig. 4 Body temperature records over time for representative individuals from each age-sex class of the western (ANKARA) and eastern (KARS) populations of Anatolian ground squirrels (*Spermophilus xanthoprimum*) before, during, and after hibernation under natural conditions. The selected individuals are those whose hibernation durations were closest to the mean values for their respective groups. Solid lines indicate body temperature, while dashed black lines represent soil temperature



of lineage (Wald $\chi^2=48.799$, $df=1$, $P<0.001$), sex (Wald $\chi^2=172.043$, $df=1$, $P<0.001$), and population nested within lineage (Wald $\chi^2=219.643$, $df=8$, $P<0.001$), along with a significant interaction effect of lineage and sex (Wald $\chi^2=6.209$, $df=1$, $P=0.013$), but no significant interaction effect of population and sex nested within lineage (Wald $\chi^2=7.502$, $df=8$, $P=0.484$). Specifically, although both lineages exhibited similar degrees of variation in body size across sexes, the eastern lineage was morphologically larger than the western lineage, particularly among males (Fig. 5).

Discussion

This study adopts a novel approach by simultaneously examining the bioclimatic niche, hibernation patterns, and body size of Anatolian ground squirrels (*Spermophilus xanthoprimum*), three key ecological, physiological, and

morphological traits that have rarely been studied in combination. By integrating ecological niche modeling (estimating bioclimatic niche using presence data), physiological monitoring (recording Tb using implanted data loggers), and morphological analysis (estimating body size using geometric morphometrics) across multiple populations, this study provides a comprehensive understanding of how elevational and associated climatic gradients shape phenotypic variation in Anatolian ground squirrels. To our knowledge, this is the first study to combine these three trait dimensions using three distinct methodologies within a single framework for any hibernating mammal.

The distribution ecology of Anatolian ground squirrels has previously been studied using ecological niche modelling (Gür 2013, 2022). These studies demonstrated that climate is one of the main factors limiting the geographic distribution of Anatolian ground squirrels and therefore they represent an ideal study system for ecological niche

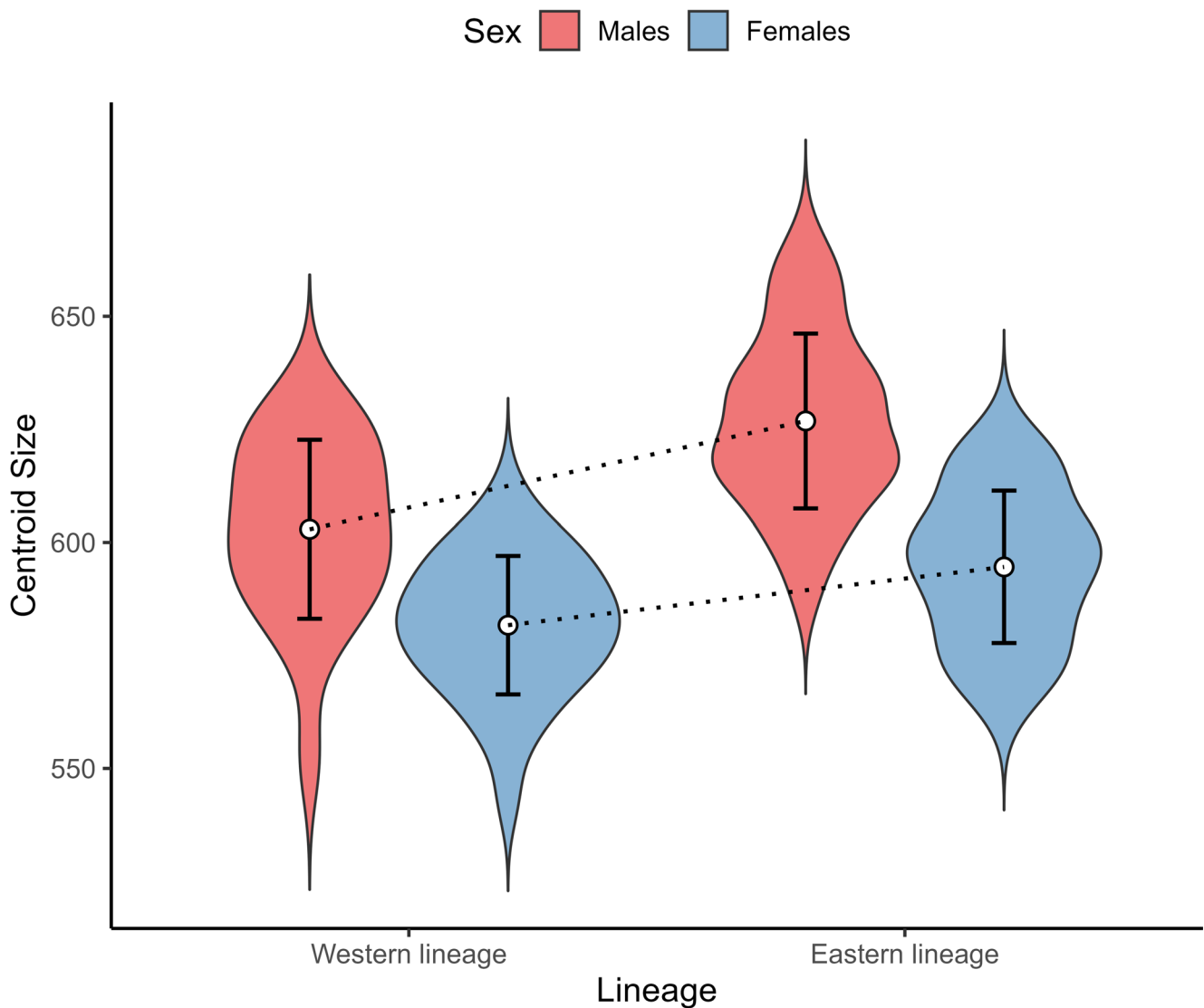


Fig. 5 Variation in body size in Anatolian ground squirrels (*Spermophilus xanthopyrmnus*) based on centroid size across the western and eastern lineages. Violin plots represent the distribution of body size for males and females within each lineage. White-filled circles indicate mean values, and vertical bars denote standard deviations. Dotted lines

connect the mean values for each sex across both lineages to facilitate comparison. Note that the dotted lines are not parallel; the female-to-male difference is larger in the eastern lineage than in the western lineage, visually underscoring the greater male size increase in the east

modelling. In these studies, as well as in most other studies (Smith et al. 2019), niche models have typically been constructed at the species level, treating the species as a single, undifferentiated entity responding to environmental conditions. This approach overlooks whether present data represent a single evolutionary unit or a set of independent evolutionary units, each differing in its respective niche. Yet, as is evident, divergence in the bioclimatic niche within Anatolian ground squirrels has not been studied. This study fills this gap by examining differences in the bioclimatic niches of two deeply divergent parapatric cyt b mtDNA lineages distributed along a west-east axis across central and eastern Anatolia. Our results indicate that the bioclimatic

niches of both lineages are not equivalent. However, this pattern appears to result from the underlying bioclimatic differences between the regions the western and eastern lineages inhabit. Specifically, the eastern lineage inhabits areas at higher elevations with colder, wetter, and more seasonally variable environments than the western lineage. These findings suggest that both lineages track the bioclimatic conditions available in their respective ranges, with no evidence supporting intrinsic niche divergence. However, beyond methodological considerations (Warren et al. 2008; Broennimann et al. 2012), interpreting these results relies on the assumption that cyt b mtDNA lineages accurately represent independent evolutionary units within Anatolian

ground squirrels, reflecting biologically meaningful patterns of niche divergence. Regardless of this assumption, the fact remains that Anatolian ground squirrels inhabiting eastern Anatolia are clearly exposed to markedly different climatic conditions, which are likely to shape their physiological and morphological traits. Therefore, in this study, we further studied environmental variation in the hibernation patterns and body size of Anatolian ground squirrels.

In Anatolian ground squirrels, daily rhythmicity of Tb before and during hibernation has previously been studied in a single population under both natural and laboratory conditions (Kart Gür et al. 2009), revealing that a robust circadian Tb rhythm is present in the pre-hibernation euthermic phase, but disappears during multiday torpor bouts. Additionally, a detailed characterization of hibernation patterns, particularly focusing on age and sex differences, has been reported for the same population under natural conditions (Kart Gür and Gür 2015), showing that hibernation patterns are influenced by age-sex classes, as well as environmental conditions. While these studies provided valuable insights into hibernation in a single population, they did not address how hibernation patterns vary across populations inhabiting diverse environmental conditions. Indeed, unlike North American marmotine squirrels (Lehmer and Biggins 2005; Zervanos et al. 2010; Sheriff et al. 2011), environmental variation in the hibernation patterns of Old World ground squirrels (the genus *Spermophilus* sensu stricto, Helgen et al. 2009), including Anatolian ground squirrels, has not yet been studied under natural conditions due to the methodological challenges involved in collecting high-resolution Tb data from free-living individuals, especially across multiple populations. This study fills this gap by examining differences in the hibernation patterns of two natural populations located 880 km apart and therefore provides the first comparative analysis of environmental variation in hibernation patterns for Old World ground squirrels under natural conditions. Our results indicate that Anatolian ground squirrels from the eastern population, which inhabits a higher-elevation, colder, wetter, and more seasonally variable environment, exhibit longer hibernation periods, spend a higher proportion of this period in torpor bouts, and achieve deeper reductions in Tb than conspecifics from the western population. The observation of sub-zero intraperitoneal temperatures in one individual from the eastern population (inhabiting a more challenging environment) suggests that, under certain conditions, Anatolian ground squirrels may be capable of supercooling during hibernation, a phenomenon known to occur in at least a few other marmotine squirrels (Barnes 1989; Hut et al. 2002). Additionally, adult males emerge earlier and at a greater body mass, exhibit shorter hibernation periods and spend a smaller proportion of this period in torpor bouts than the other age-sex classes. Given

that areas at higher elevations with colder and more seasonally variable environments typically experience harsher and longer winters with increased energy demands and prolonged periods of food scarcity, physiological strategies such as extended hibernation and greater reliance on deeper, longer-lasting torpor bouts likely enable marmotine squirrels inhabiting these environmental conditions to conserve energy more efficiently (as discussed further below).

Geographic variation in the body size of Anatolian ground squirrels in relation to environmental variables has already been studied in detail. In that study, variation in body size was analyzed at the population and sex levels (Gür 2010). Thus, this study extends that study by examining how population- and sex-level variation is structured at the lineage level. By analyzing variation in body size at the lineage level, this study provides a complementary and more integrative perspective, particularly given that environmental variation in the bioclimatic niche and the hibernation patterns, are also investigated at the lineage level. This integrative approach allows us to better understand the broader evolutionary and ecological context shaping phenotypic variation. Our results indicate that Anatolian ground squirrels from the eastern lineage, which inhabits areas at higher elevations with colder, wetter, and more seasonally variable environments, are morphologically larger than conspecifics from the western lineage, particularly among males. Many species of marmotine squirrels hibernate for up to 8–9 months each year. They rely primarily on fat reserves as a source of energy during hibernation. Accordingly, overwinter survival is positively correlated with the amount of fat stored prior to hibernation (*Marmota*: Armitage 2003; *Cynomys*: Hoogland 2003; *Spermophilus*: Yensen and Sherman 2003). However, in fat-storing hibernating mammals, the maximum amount of fat that can be stored is typically constrained to 40–50% of body mass, due to morphological limitations and costs associated with fat storage. Consequently, fat storage capacity scales proportionally with body size (Humphries et al. 2003, 2004). In colder and more seasonally variable regions, such as those the eastern lineage inhabits, where winter energy demands are higher and food scarcity persists for prolonged periods, individuals, particularly adult males (see below), are expected to exhibit greater winter starvation resistance. This, in turn, necessitates increased fat accumulation prior to hibernation, which requires a morphologically larger body. In other words, greater winter starvation resistance may favour large body size (Boyce 1978; Lindstedt and Boyce 1985; Millar and Hickling 1990; Gür 2010; Gür and Kart Gür 2012). A similar pattern is also observed within species across age-sex classes. Differences between adult males and the other age-sex classes (Young 1990; Michener 1992; Gür and Kart Gür 2005; Buck et al. 2008; Healy et al. 2012; Kart Gür and

Gür 2015), such as exhibiting shorter hibernation periods and spending a smaller proportion of this period in torpor bouts, suggest that adult males follow a less energy-conserving strategy and exhibit greater winter starvation resistance (French 1982, 1988; Gür 2010; Gür and Kart Gür 2012). This pattern is possibly linked to trade-offs between the energy-saving benefits of torpor bouts and the reproductive benefits gained by terminating hibernation earlier (Healy et al. 2012). Indeed, Anatolian ground squirrels, particularly males, from the eastern lineage are morphologically larger, consistent with the demands of their more energetically challenging environment. Taken together, while environmental variation in body size likely reflects adaptation to increased energetic demands in colder and more seasonally variable environments, demographic variation (differences between sexes) in body size is likely shaped, at least in part, by trade-offs between hibernation and reproduction, which further accentuate differences between females and males within these environments.

Overall, our results demonstrate that elevational and climatic gradients shape phenotypic variation in Anatolian ground squirrels through lineage-, population-, and demographic-level responses. Consistent with our hypothesis, we detected congruent patterns of environmental variation in bioclimatic niche, hibernation patterns, and body size, suggesting coordinated adaptive responses to environmental conditions. By jointly analyzing these trait dimensions, our study underscores the value of an integrative approach for understanding eco-evolutionary divergence in hibernating mammals.

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Declarations

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

References

- Animal Care and Use Committee (1998) Guidelines for the capture, handling, and care of mammals as approved by the American society of mammalogists. *J Mammal* 79:1416–1431
- Armitage KB (2003) Marmots: *Marmota Monax* and allies. In: Feldhamer GA, Thompson BC, Chapman JA (eds) *Wild Mammals of North America: biology, management, and conservation*. Johns Hopkins University Press, Baltimore, pp 188–210
- Barnes BM (1989) Freeze avoidance in a mammal: body temperatures below 0°C in an arctic hibernator. *Science* 244:1593–1595
- Bennet E (1835) Mammals of the neighbourhood of Trebizond and Erzeroum. *Proc Zool Soc London* 89–90.
- Bergmann C (1847) Ueber die verhältnisse der wärmeökonomie der Thiere Zu ihrer grösse. *Göttinger Studien* 1:595–708
- Bookstein FL (1991) *Morphometric tools for landmark data: geometry and biology*. Cambridge University Press, Cambridge
- Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol Model* 275:73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>
- Boyce MS (1978) Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. *Oecologia* 36:1–19
- Broennimann O, Fitzpatrick MC, Pearman PB et al (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Glob Ecol Biogeogr* 21:481–497
- Brown JL, Bennett JR, French CM (2017) SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ* 5:e4095. <https://doi.org/10.7717/peerj.4095>
- Buck CL, Breton A, Kohl F, Tøien Ø, Barnes BM (2008) Overwinter body temperature patterns in free-living Arctic squirrels (*Spermophilus parryii*). In: Lovegrove BG, McKechnie AE (eds) *Hypometabolism in animals: hibernation, torpor and cryobiology*. University of KwaZulu-Natal Press, South Africa
- Darwin C (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London
- Di Cola V, Broennimann O, Petitpierre B et al (2017) Ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography* 40:774–787
- Dryden IL, Mardia KV (1998) *Statistical analysis of shape*. Wiley, Chichester
- Dumlupınar İ, Gür H, Özüdoğru B (2023) Distributional ecology of *Noccaea vesicaria* in relation to the Anatolian diagonal. *Turk J Bot* 47:267–277
- Dunbar MB, Brigham RM (2010) Thermoregulatory variation among populations of bats along a latitudinal gradient. *J Comp Physiol B* 180:885–893. <https://doi.org/10.1007/s00360-010-0457-y>
- Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>

- French AR (1982) Intraspecific differences in the pattern of hibernation in the ground squirrel *Spermophilus beldingi*. *J Comp Physiol B* 148:83–91
- French AR (1988) The patterns of mammalian hibernation. *Am Sci* 76:569–575
- Gould SJ, Johnston RF (1972) Geographic variation. *Annu Rev Ecol Syst* 3:457–498
- Gündüz İ, Jaarola M, Tez Ç et al (2007) Multigenic and morphometric differentiation of ground squirrels (*Spermophilus*, sciuridae, Rodentia) in turkey, with a description of a new species. *Mol Phylogenet Evol* 43:916–935
- Gür H (2010) Why do Anatolian ground squirrels exhibit a Bergmannian size pattern? A phylogenetic comparative analysis of geographic variation in body size. *Biol J Linn Soc* 100:695–710
- Gür H (2013) The effects of late quaternary glacial–interglacial cycles on Anatolian ground squirrels: range expansion during the glacial periods? *Biol J Linn Soc* 109:19–32
- Gür H (2016) The anatolian diagonal revisited: testing the ecological basis of a biogeographic boundary. *Zool Middle East* 62:189–199. <https://doi.org/10.1080/09397140.2016.1226544>
- Gür H (2019) *Tür Dağılım Modellemesi ile İklim Değişikliği Uygulamaları*. Ekoloji ve Evrimsel Biyoloji Derneği Yayınları No. 1. <https://ekoeco.org/wp-content/uploads/2025/06/REkoloji.pdf>
- Gür H (2022) The future impact of climate and land-use changes on Anatolian ground squirrels under different scenarios. *Ecol Inf* 70:101725. <https://doi.org/10.1016/j.ecoinf.2022.101725>
- Gür H, Kart Gür M (2005) Annual cycle of activity, reproduction, and body mass of Anatolian ground squirrels (*Spermophilus xanthoprimum*) in Turkey. *J Mammal* 86:7–14
- Gür H, Kart Gür M (2012) Is spatial variation in food availability an explanation for a Bergmannian size pattern in a North American hibernating, burrowing mammal? An information-theoretic approach. *J Zool* 287:104–114
- Gür H, Perkaş U, Kart Gür M (2018) Do climate-driven altitudinal range shifts explain the intraspecific diversification of a narrow ranging montane mammal, Taurus ground squirrels? *Mammal Res* 63:197–211. <https://doi.org/10.1007/s13364-017-0345-x>
- Hammer Ø, Harper DAT (2001) Past: paleontological statistics software package for education and data analysis. *Palaeontol Electron* 4:1–9
- Healy JE, Burdett KA, Buck CL, Florant GL (2012) Sex differences in torpor patterns during natural hibernation in golden-mantled ground squirrels (*Callospermophilus lateralis*). *J Mammal* 93:751–758. <https://doi.org/10.1644/11-MAMM-A-329.1>
- Helgen KM, Cole FR, Helgen LE, Wilson DE (2009) Generic revision in the holarctic ground squirrel genus *Spermophilus*. *J Mammal* 90:270–305
- Hoogland JL (2003) Black-tailed prairie dog: *Cynomys ludovicianus* and allies. In: Feldhamer GA, Thompson BC, Chapman JA (eds) *Wild mammals of North America: biology, management, and conservation*, 2nd edn. Johns Hopkins University, Baltimore, pp 232–247
- Humphries MM, Thomas DW, Kramer DL (2003) The role of energy availability in mammalian hibernation: a cost-benefit approach. *Physiol Biochem Zool* 76:165–179. <https://doi.org/10.1086/367950>
- Humphries MM, Umbanhowar J, McCann KS (2004) Bioenergetic prediction of climate change impacts on Northern mammals. *Integr Comp Biol* 44:152–162. <https://doi.org/10.1093/icb/44.2.152>
- Hut R, Barnes BM, Daan S (2002) Body temperature patterns before, during, and after semi-natural hibernation in the European ground squirrel. *J Comp Physiol B* 172:47–58
- Institute for Laboratory Animal Research-ILAR (1996) *Guide for the care and use of laboratory animals*. National Academy, Washington
- Jarvis A, Reuter HI, Nelson A, Guevara E (2008) Hole-filled seamless SRTM data V4. International Centre for Tropical Agriculture (CIAT). <https://srtm.csi.cgiar.org>
- Karabağ T (1953) The biology of ground squirrels (Citellus) near Ankara with methods for their control. Publications of the Agricultural Faculty of Ankara University, Ankara
- Karger DN, Conrad O, Böhrner J et al (2017a) Climatologies at high resolution for the earth's land surface areas. *Sci Data* 4:170122. <https://doi.org/10.1038/sdata.2017.122>
- Karger DN, Conrad O, Böhrner J et al (2017b) Data from: climatologies at high resolution for the earth's land surface areas. Dryad Digit Repository. <https://doi.org/10.5061/dryad.kd1d4>
- Kart Gür M, Gür H (2010) *Spermophilus xanthoprimum* (Rodentia: Sciuridae). *Mammalian Species* 42:183–194. <https://doi.org/10.1644/907.1>
- Kart Gür M, Gür H (2015) Age and sex differences in hibernation patterns in free-living Anatolian ground squirrels. *Mamm Biol* 80:265–272
- Kart Gür M, Refinetti R, Gür H (2009) Daily rhythmicity and hibernation in the Anatolian ground squirrel under natural and laboratory conditions. *J Comp Physiol B* 179:155–164. <https://doi.org/10.1007/s00360-008-0294-4>
- Kass JM, Vilela B, Aiello-Lammens ME, Muscarella R, Merow C, Anderson RP (2018) Wallace: a flexible platform for reproducible modeling of species niches and distributions built for community expansion. *Methods Ecol Evol* 9:1151–1156
- Klingenberg CP (2011) MorphoJ: an integrated software package for geometric morphometrics. *Mol Ecol Resour* 11:353–357. <https://doi.org/10.1111/j.1755-0998.2010.02924.x>
- Kryštufek B, Vohralík V (2005) *Mammals of Turkey and cyprus*. Rodentia I: sciuridae, dipodidae, gliridae, arvicolinae. Založba Annales, Koper
- Kryštufek B, Vohralík V (2012) Taxonomic revision of the palaeartic rodents (Rodentia). Sciuridae: Xerinae 1 (*Eutamias* and *Spermophilus*). *Lynx* 43:17–111
- Lee TE, Barnes BM, Buck CL (2009) Body temperature patterns during hibernation in a free-living Alaska marmot (*Marmota flaviventris*). *Ethol Ecol Evol* 21:403–413. <https://doi.org/10.1080/08927014.2009.9522495>
- Lehmer EM, Biggins DE (2005) Variation in torpor patterns of free-ranging black-tailed and Utah prairie dogs across gradients of elevation. *J Mammal* 86:15–21. [https://doi.org/10.1644/1545-1542\(2005\)086%3C;0015:VITPOF%3E;2.0.CO;2](https://doi.org/10.1644/1545-1542(2005)086%3C;0015:VITPOF%3E;2.0.CO;2)
- Lindstedt SL, Boyce MS (1985) Seasonality, fasting endurance, and body size in mammals. *Am Nat* 125:873–878. <https://doi.org/10.1086/284385>
- Mayr E (1956) Geographical character gradients and climatic adaptation. *Evolution* 10:105–108. <https://doi.org/10.1111/j.1558-5646.1956.tb02836.x>
- Mazel F, Wüest RO, Gueguen M et al (2017) The geography of ecological niche evolution in mammals. *Curr Biol* 27:1369–1374. <https://doi.org/10.1016/j.cub.2017.03.081>
- McCullagh P, Nelder JA (1989) *Generalized linear models*, 2nd edn. Chapman and Hall/CRC, London
- McNab BK (2002) *The physiological ecology of vertebrates: A view from energetics*. Cornell University Press, Ithaca
- Meiri S, Dayan T (2003) On the validity of Bergmann's rule. *J Biogeogr* 30:331–351. <https://doi.org/10.1046/j.1365-2699.2003.00837.x>
- Michener GR (1992) Sexual differences in overwinter torpor patterns of richardson's ground squirrels in natural hibernacula. *Oecologia* 89:397–406. <https://doi.org/10.1007/BF00317415>
- Millar JS, Hickling GJ (1990) Fasting endurance and the evolution of mammalian body size. *Funct Ecol* 4:5–12. <https://doi.org/10.2307/2389646>

- Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models. *Methods Ecol Evol* 5:1198–1205
- Osorio-Olvera L, Lira-Noriega A, Soberón J et al (2020) NTBOX: an R package with graphical user interface for modelling and evaluating multidimensional ecological niches. *Methods Ecol Evol* 11:1199–1206. <https://doi.org/10.1111/2041-210X.13452>
- Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol Model* 213:63–72. <https://doi.org/10.1016/j.ecolmodel.2007.11.008>
- Peterson AT, Soberón J, Pearson RG et al (2011) Ecological niches and geographic distributions. Princeton University Press, Princeton
- Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME (2017) Opening the black box: an open-source release of maxent. *Ecography* 40:887–893. <https://doi.org/10.1111/ecog.03049>
- Rohlf FJ (2010) TpsDig, version 2.16. Department of Ecology and Evolution, State University of New York at Stony Brook
- Ruf T, Arnold W (2000) Mechanisms of social thermoregulation in hibernating alpine marmots (*Marmota marmota*). In: Heldmaier G, Klingenspor M (eds) *Life in the Cold*. Springer-Verlag, Heidelberg
- Ruf T, Geiser F (2014) Daily torpor and hibernation in birds and mammals. *Biol Rev* 90:891–926. <https://doi.org/10.1111/brv.12137>
- Sheriff MJ, Kenagy GJ, Richter M et al (2011) Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. *Proc R Soc Lond B Biol Sci* 278:2369–2375. <https://doi.org/10.1098/rspb.2010.2482>
- Smith AB, Godsoe W, Rodríguez-Sánchez F et al (2019) Niche Estimation above and below the species level. *Trends Ecol Evol* 34:260–273. <https://doi.org/10.1016/j.tree.2018.12.005>
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*. W.H. Freeman and Company, New York, NY
- Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62:2868–2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x>
- Yensen E, Sherman PW (2003) Ground squirrels (*Spermophilus* species and *Ammospermophilus* species). In: Feldhamer GA, Thompson BC, Chapman JA (eds) *Wild mammals of North America: biology, management, and conservation*, 2nd edn. Johns Hopkins University, Baltimore, pp 211–231
- Young PJ (1990) Hibernating patterns of free-ranging Columbian ground squirrels. *Oecologia* 83:504–511. <https://doi.org/10.1007/BF00317204>
- Zervanos SM, Salsbury CM (2003) Seasonal body temperature fluctuations and energetic strategies in free-ranging Eastern woodchucks (*Marmota monax*). *J Mammal* 84(1):299–310. [https://doi.org/10.1644/1545-1542\(2003\)084%3C;0299:SBTFAE%3E;2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084%3C;0299:SBTFAE%3E;2.0.CO;2)
- Zervanos SM, Maher CR, Waldvogel JA, Florant GL (2010) Latitudinal differences in the hibernation characteristics of woodchucks (*Marmota monax*). *Physiol Biochem Zool* 83:135–141. <https://doi.org/10.1086/648736>

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