HACETTEPE JOURNAL OF BIOLOGY AND CHEMISTRY

Review Article

Hacettepe J. Biol. & Chem., 2010, 38 (3) 247-253

Anatolian Ground Squirrels (*Spermophilus xanthoprymnus*): Hibernation and Geographic Variation of Body Size in a Species of Old World Ground Squirrels

Hakan Gür and Mutlu Kart Gür

Ahi Evran University, Faculty of Arts and Science, Department of Biology, Kırşehir, Turkey

INTRODUCTION

Old world ground squirrels (the genus *Spermophilus* sensu stricto), including 14 species, are one of the eight genera of ground squirrels previously included within the genus *Spermophilus* sensu lato (Helgen et al., 2009), which is among the most intensively studied groups of mammals with respect to its behaviour, ecology, and evolution. Among these genera of ground squirrels, only the genus *Spermophilus* sensu stricto (hereafter, *Spermophilus*) is restricted to Eurasia (Helgen et al., 2009). Old world ground squirrels (*Spermophilus*) are group-living, diurnal, hibernating marmotine sciurids inhabiting open habitats (grasslands, deserts, and tundra). They spend the majority of their lives sleeping and hibernating in underground burrows.

Three species of old world ground squirrels (Anatolian ground squirrels – *Spermophilus xanthoprymnus*, European ground squirrels – *Spermophilus citellus*, and Taurus ground squirrels – *Spermophilus taurensis*) are native to Turkey. Anatolian ground squirrels are endemic to Turkey and small areas nearby, where they are distributed in central lowland and eastern highland Anatolia and in small areas in adjacent Armenia and northwestern Iran. They are also known from a few localities in southern Anatolia, in both the Teke peninsula and Çukurova plain (Kart Gür and Gür, 2010). European ground squirrels are distributed in eastern Europe, including the European part of Turkey west of the Bosphorus (Mitchell-Jones et al., 1999). Taurus ground squirrels are distributed in the Anatolian part of Turkey, in the eastern part of the western Taurus Mountains, and are parapatric with Anatolian ground squirrels at the northernmost limit of their distribution area (Fig. 1—Gündüz et al., 2007; Özkurt et al., 2007).

We have been studying the physiological and evolutionary ecology of Anatolian ground squirrels, *S. xanthoprymnus*, one of three species of old world ground squirrels native to Turkey, for about 10 years (Gür, 2001; 2007; 2010; Gür and Barlas, 2006; Gür and Kart Gür, 2005; Kart, 2000; Kart Gür, 2008; Kart Gür and Gür, 2010; Kart Gür et al., 2009). As in many other species of old world ground squirrels, Anatolian ground squirrels are obligately hibernating marmotine sciurids overwintering in underground burrows. *S. xanthoprymnus* primarily inhabits steppes and alpine meadows throughout its distribution area. Although lengths of the hibernation and active seasons vary among years and geographic populations depending on local environmental conditions, Anatolian ground squirrels are mainly active from March through September, and hibernate during the remaining months.

Here we just briefly combine our findings about hibernation and patterns of geographic variation in body size and their relationship to a suite of interacting environmental variables. To date, our findings are the most comprehensive ones available on these topics in old world ground squirrels. Some of the potential strengths of these studies are as follows: (i) we determined hibernation patterns of Anatolian ground squirrels under both natural and laboratory conditions, with special attention to age and sex differences (Kart Gür, 2008; Kart Gür et al., 2009) and (ii) we used a phylogenetic comparative method (Martins and Hansen's (1997) phylogenetic generalized least-squares analysis, PGLS) to deal with patterns of geographic variation in body size of Anatolian ground squirrels (Gür, 2007; 2010). Phylogenetic comparative analyses were used because intraspecific comparative datasets, like interspecific ones, may contain significant amounts of phylogenetic signal, suggesting that intraspecific comparative studies should also incorporate phylogenetic information (Ashton, 2004), to take into account phylogenetic nonindependence of samples and then to estimate correctly the Type I error of statistical analyses (Diniz-Filho et al., 2007). Populations of *S. xanthoprymnus* show clear phylogeographic structuring, with subdivision into five cytochrome *b* lineages (Gündüz et al., 2007), thereby justifying using phylogenetic comparative analyses.

Hibernation patterns of Anatolian ground squirrels were determined with temperature-sensitive data loggers implanted intraperitoneally under general anesthesia. Differences in hibernation patterns between age and sex classes were studied (note that here we just briefly mention hibernation patterns of free-living adult males and females in steppe habitat 50 km south of Ankara, Turkey—Kart Gür, 2008; Kart Gür et al., 2009). For use in analyses of geographic variation in body size, adult Anatolian ground squirrels were collected from 10 geographic localities in Anatolia, covering most of their distribution area. The phylogenetic relationships among sampled populations of *S. xanthoprymnus* were estimated from the cytochrome *b* mtDNA sequences from Harrison et al. (2003) and Gündüz et al. (2007). Four principal hypotheses were tested to understand the possible cause(s) of the observed pattern of geographic variation in body size (Gür, 2007; 2010): (i) heat conservation hypothesis (Bergmann, 1847 in James, 1970; traditionally appended to Rensch's (1938) and Mayr's (1956; 1963) intraspecific formulation of Bergmann's rule), (ii) heat dissipation hypothesis (James' intraspecific formulation of Bergmann's rule; Aldrich and James, 1991; James, 1970; 1991; see also Hamilton, 1961), (iii) primary productivity hypothesis (Rosenzweig, 1968), and (iv) seasonality hypothesis (Boyce, 1978; Lindstedt and Boyce, 1985; Millar and Hickling, 1990). These explanations all assume that patterns of geographic variation in body size are the result of natural selection (Ashton et al., 2000).

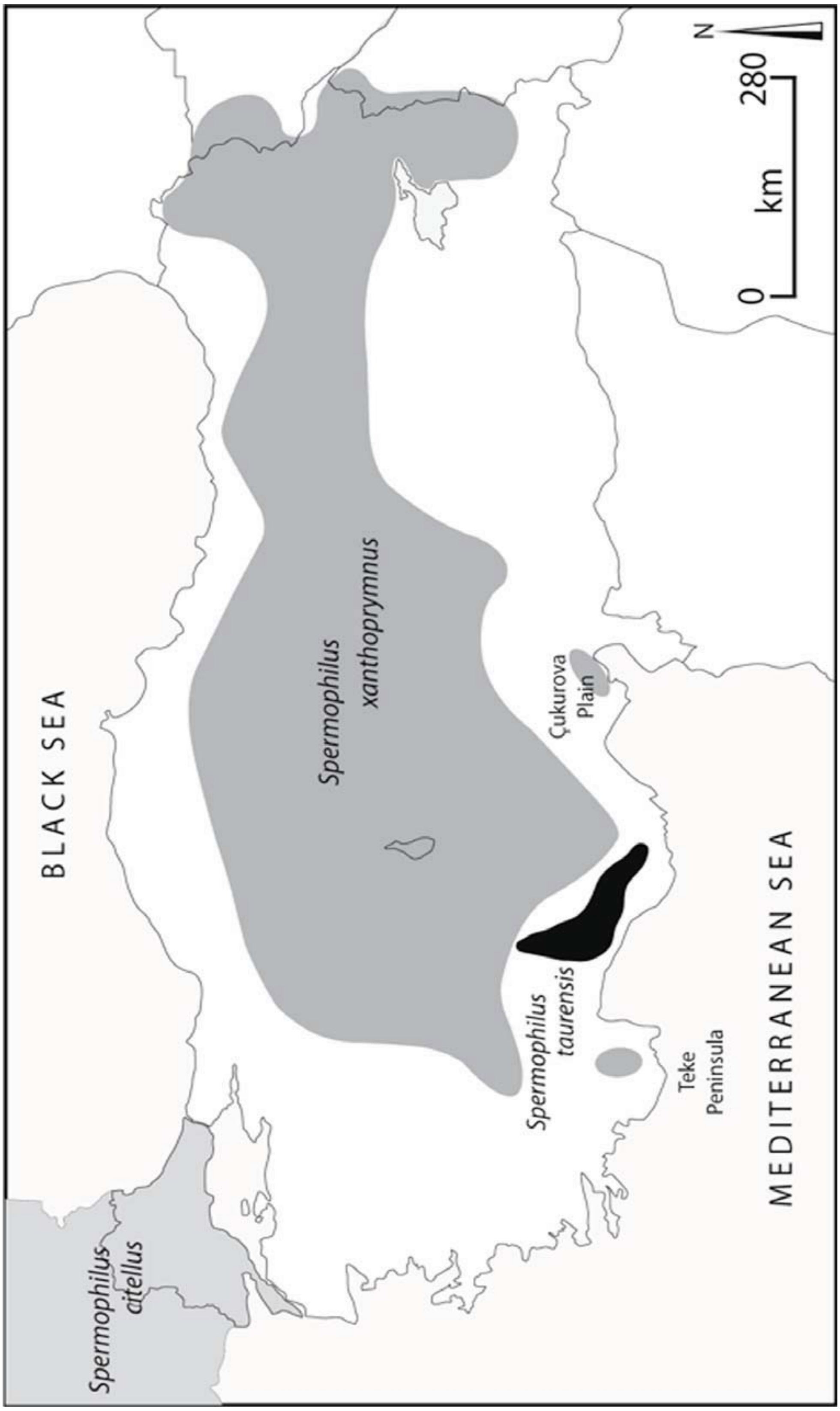

Figure 1. Geographic ranges of three species of old world ground squirrels native to Turkey.

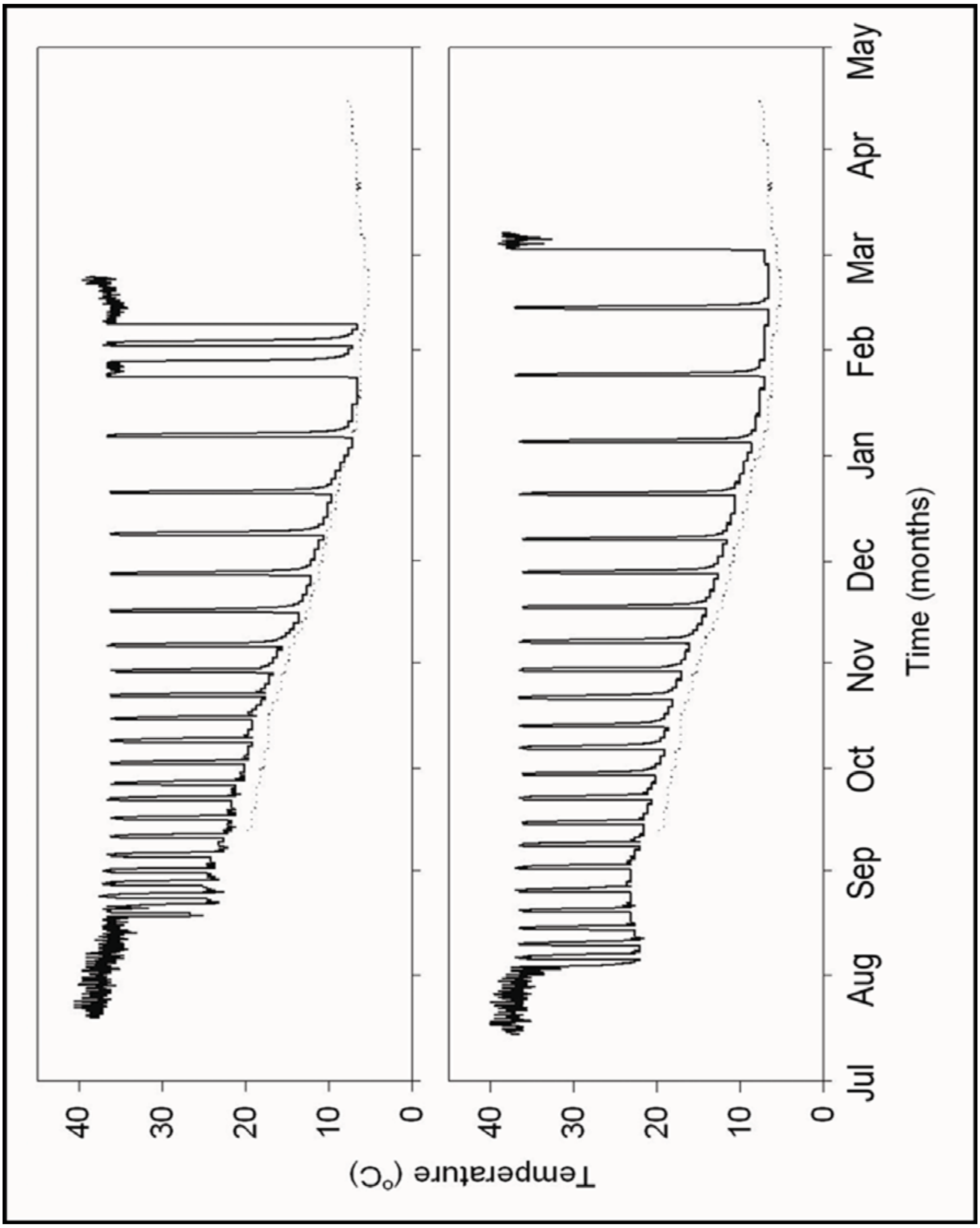

Figure 2. Body temperature records of representative adult male (above) and female (below) Anatolian ground squirrels before, during, and after the heterothermal season. *Dashed lines* indicate soil temperature at 1 m depth, which is the expected depth of the hibernacula.

In Anatolian ground squirrels, starting in the late summer or early autumn and ending in the late winter or early spring, body temperature is repeatedly lowered from the euthermic level down to the temperature of the surroundings in a series of torpor bouts (periods of low body temperature lasting longer than 24 h), each lasting from several days to several weeks. The interval during which an animal exhibits torpor bouts is defined as the heterothermal (or hibernation) season. Adult males have shorter heterothermal seasons than adult females (mean, 168 days vs. 212 days), beginning heterothermy (or hibernation) later (mean, 31 August vs. 11 August), and ending earlier (mean, 14 February vs. 10 March; Figure 2). Regardless of the absolute duration of heterothermy, torpor bouts account for a smaller proportion of the heterothermal season in adult males than in adult females (mean, % 86 vs. % 91—Kart Gür, 2008).

Anatolian ground squirrels exhibit considerable geographic variation in body size (estimated from skull characters). Interlocality differences account for about 65% of the variation in body size of adult males and females. In both sexes, body size increases towards colder, more seasonal environments with higher summer precipitation and productivity, towards northeastern highland Anatolia. It is thus important to note here that Anatolian ground squirrels exhibit a Bergmannian size pattern: increasing body size with decreasing ambient temperature. In males, but not in females, populations from more seasonal northeastern highland Anatolia show the greatest degree of differentiation, indicating that both sexes exhibit slightly different patterns of geographic variation in body size. The most important factors driving geographic size variation are summer precipitation and seasonality for males (as predicted by primary productivity and seasonality hypotheses, respectively) and summer precipitation for females (as predicted by primary productivity hypothesis— Gür, 2007; 2010).

Hibernating species of the genera of ground squirrels (*Spermophilus* sensu lato) rely on fat reserves as the source of energy during hibernation. Consequently, over-winter survival is positively correlated with pre-hibernation fat reserves (Yensen and Sherman, 2003). However, for fat-storing hibernators, because of both morphological constraints and costs associated with fat storage, the maximum size of fat reserves is consistently 40-50% of total body mass and therefore the capacity to store fat increases proportionately with body mass (Humphries et al., 2003; 2004). Because large individuals store more fat prior to hibernation and deplete their fat reserves less rapidly (French, 1988), they may be more likely to survive over-winter (including immediately following hibernation) in seasonal environments where severe winters and long periods of food shortage occur. In other words, over-winter fasting endurance may favour large body size (Boyce, 1978; Lindstedt and Boyce, 1985; Millar and Hickling, 1990). But large body size is possible only if food availability during the growing season is sufficiently high to meet the energetic costs of that size (McNab, 2002). Because food availability during the growing season may influence over-winter fasting endurance through its effect on body size, especially in hibernating species of the genera of ground squirrels and other fat-storing hibernators, food availability (primary productivity hypothesis) and over-winter fasting endurance (seasonality hypothesis) may not be mutually exclusive. Food availability and, especially in males, over-winter fasting endurance are thus likely the primary underlying mechanisms generating the observed pattern of geographic variation in body size (or a Bergmannian size pattern—Gür, 2007; 2010).

As understood from sex differences in hibernation patterns between adults (see Fig. 2), obviously adult males remain active longer especially during the late winter/early spring when soil temperature at the depth of the hibernaculum, and presumably also sleeping chambers, is at or near the lowest value and food is still scarce (Kart Gür, 2008; Kart Gür et al., 2009). They therefore run more risk of starving, especially in more seasonal environments. This may explain why males and females respond differently to seasonality of the environment (note that seasonality hypothesis received support in males only) and therefore exhibit slightly different patterns of geographic variation in body size. As expected, sexual size dimorphism, too, varies geographically and appears to increase towards more seasonal northeastern highland Anatolia (Gür, 2007; 2010).

In *S. xanthoprymnus*, cytochrome *b* lineages have signals of recent range expansion. Consequently, Gündüz et al. (2007) claim that Anatolian ground squirrels survived the last glacial maximum (LGM) in small suitable habitats (refugia), and that the postglacial recolonization of Anatolia arouse from these LGM refugia. Recent range expansion from these LGM refugia suggests that the current geographic pattern of size variation in *S. xanthoprymnus* is mostly due to recent (i.e., postglacial) adaptive processes. Accordingly, although part of the variation is phylogenetically structured (as estimated using the PGLS parameter α values), the strong association between body size and environment is observed, suggesting that adaptive processes in addition to historical ones have contributed to the evolution of body size (Gür, 2007; 2010).

ACKNOWLEDGEMENTS

We extend our thanks to the editor, Ergi Deniz Özsoy, for inviting us to contribute a small review to this special issue of Hacettepe Journal of Biology and Chemistry. We thank Atıl Barış Albayrak and Utku Perktaş for drawing Figure 1.

REFERENCES

Aldrich JW, James FC. 1991. Ecogeographic variation in the American robin (*Turdus migratorius*). Auk 108: 230–249.

Ashton KG. 2004. Comparing phylogenetic signal in intraspecific and interspecific body size datasets. Journal of Evolutionary Biology 17: 1157–1161.

Ashton KG, Tracy MC, de Queiroz A. 2000. Is Bergmann's rule valid for mammals? American Naturalist 156: 390–415.

Boyce MS. 1978. Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. Oecologia 36: 1–19.

Diniz-Filho JAF, Bini LM, Rodríguez MA, Rangel TFLVB, Hawkins BA. 2007. Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnivora. Ecography 30: 598–608.

French AR. 1988. The patterns of mammalian hibernation. American Scientist 76: 569–575.

Gündüz İ, Jaarola M, Tez Ç, Yeniyurt C, Polly PD, Searle JB. 2007. Multigenic and morphometric differentiation of ground squirrels (*Spermophilus*, Sciuridae, Rodentia) in Turkey, with a description of a new species. Molecular Phylogenetics and Evolution 43: 916–935.

Gür H. 2001. Population biology of *Spermophilus xanthoprymnus* (Rodentia: Sciuridae). M.Sc. thesis, Hacettepe University, Ankara, Turkey.

Gür H. 2007. Morphometric variation in Anatolian ground squirrel (*Spermophilus xanthoprymnus*) and its relationship to selected environmental variables. Ph.D. thesis, Hacettepe University, Ankara, Turkey.

Gür H. 2010. Why do Anatolian ground squirrels exhibit a Bergmannian size pattern? A phylogenetic comparative analysis of geographic variation in body size. Biological Journal of the Linnean Society 100: 695-710.

Gür H, Barlas N. 2006. Sex ratio of a population of Anatolian ground squirrels *Spermophilus xanthoprymnus* in Central Anatolia, Turkey. Acta Theriologica 51: 61–67.

Gür H, Kart Gür M. 2005. Annual cycle of activity, reproduction, and body mass of Anatolian ground squirrels (*Spermophilus xanthoprymnus*) in Turkey. Journal of Mammalogy 86: 7–14.

Hamilton TH. 1961. The adaptive significances of intraspecific trends of variation in wing length and body size among bird species. Evolution 15: 180–195.

Harrison RG, Bogdanowicz SM, Hoffmann RS, Yensen E, Sherman PW. 2003. Phylogeny and evolutionary history of the ground squirrels (Rodentia: Marmotinae). Journal of Mammalian Evolution 10: 249–276.

Helgen KM, Cole FR, Helgen LE, Wilson DE. 2009. Generic revision in the Holarctic ground squirrel genus *Spermophilus*. Journal of Mammalogy 90: 270–305.

Humphries MM, Thomas DW, Kramer DL. 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. Physiological and Biochemical Zoology 76: 165–179.

Humphries MM, Umbanhowar J, McCann KS. 2004. Bioenergetic prediction of climate change impacts on northern mammals. Integrative and Comparative Biology 44: 152–162.

James FC. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51: 365–390.

James FC. 1991. Complementary descriptive and experimental studies of clinal variation in birds. American Zoologist 31: 694–706.

Kart, M. 2000. The investigation of hibernation on *Spermophilus xanthoprymnus* from behavioral and biochemical points of view. M.Sc. thesis, Hacettepe University, Ankara, Turkey.

Kart Gür M. 2008. Hibernation pattern of Anatolian ground squirrel (*Spermophilus xanthoprymnus*). Ph.D. thesis, Hacettepe University, Ankara, Turkey.

Kart Gür M, Gür H. 2010. *Spermophilus xanthoprymnus* (Rodentia: Scuirdea). Mammalian Species 42: 183-194.

Kart Gür M, Refinetti R, Gür H. 2009. Daily rhythmicity and hibernation in the Anatolian ground squirrel under natural and laboratory conditions. Journal of Comparative Physiology B 179: 155–164.

Lindstedt SL, Boyce MS. 1985. Seasonality, fasting endurance, and body size in mammals. American Naturalist 125: 873–878.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. American Naturalist 149: 646–667.

Mayr E. 1956. Geographical character gradients and climatic adaptation. Evolution 10: 105–108.

Mayr E. 1963. Animal species and evolution. Belknap Press, Cambridge.

McNab BK. 2002. The physiological ecology of vertebrates: a view from energetics. Cornell University Press, Cornell.

Millar JS, Hickling GJ. 1990. Fasting endurance and the evolution of mammalian body size. Functional Ecology 4: 5–12.

Mitchell-Jones AJ, Amori G, Bogdanowicz W, Kryštufek B, Reijnders PJH, Spitzenberger F, Stubbe M, Thissen JBM, Vohralík V, Zima J. 1999. The atlas of European mammals. T & A D Poyser Natural History, Academic Press, London.

Özkurt ŞÖ, Sözen M, Yiğit N, Kandemir İ, Çolak R, Gharkheloo MM, Çolak E. 2007. Taxonomic status of the genus *Spermophilus* (Mammalia: Rodentia) in Turkey and Iran with description of a new species. Zootaxa 1529: 1–15.

Rensch B. 1938. Some problems of geographical variation and species-formation. Proceedings of the Linnean Society of London 50: 275–285.

Rosenzweig ML. 1968. The strategy of body size in mammalian carnivores. American Midland Naturalist 80: 299–315.

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. Johns Hopkins University Press, Baltimore, 211–231.