CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group

Edited by

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***Testudo graeca* Linnaeus 1758 (Eastern Subspecies Clades: *Testudo g. armeniaca, Testudo g. buxtoni, Testudo g. ibera, Testudo g. terrestris, Testudo g. zarudnyi*) – Armenian Tortoise, Zagros Tortoise, Anatolian Tortoise, Levantine Tortoise, Kerman Tortoise**

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Testudo graeca Linnaeus 1758 (Eastern Subspecies Clades: *Testudo g. armeniaca, Testudo g. buxtoni, Testudo g. ibera, Testudo g. terrestris, Testudo g. zarudnyi)* – Armenian Tortoise, Zagros Tortoise, Anatolian Tortoise, Levantine Tortoise, Kerman Tortoise

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Summary. – The eastern clades of the Spur-thighed Tortoise, *Testudo graeca* (Family Testudinidae), include small to medium-sized (maximum straightline carapace lengths [SCL] typically ≤ 30 cm, but possibly up to 46.0 cm) tortoise subspecies clades native to the Balkans (southeastern Europe) and southwestern Asia. Within this vast geographic distribution, the species occupies Mediterranean, Mediterranean-continental, and steppe climates, as well as the margins of hot deserts. In southeastern Turkey and Iran, it reaches elevations of 2500 m, the record for the species. *Testudo graeca* is characterized by the presence of a small conical keratinous spur on each posterior thigh, present in all eastern clade subspecies. The eastern clades show a very high degree of phenotypic variability, ranging from almost entirely black individuals (typically, but not exclusively in the north of its range) to yellowish (flavistic) individuals (primarily in southern Israel). They also show variability in the structure and shape of the carapace, ranging from flatter steppe forms to domed, higher-shelled forms. In general, adult females are slightly larger and heavier than males in most eastern clade regions and studied populations; however, in approximately 30% of surveyed populations across the range, males reach a similar or larger average size, and the few largest individuals recorded of the species are males. Female mean SCLs among the eastern subspecies clades range from 14.5–21.9 cm per region or population, with mean body mass ranging from ca. 700–2250 g (average ca. 1630 g); male mean SCLs range from 13.5–24.1 cm with mean body mass ranging from ca. 420–2700 g (average ca. 1560 g). Male dimorphic characters include a proportionally longer and thicker tail and plastral concavity. Females produce 1–3 clutches of 2–19 eggs annually between May and July. The species is still relatively common and widespread in a large part of its range. Some populations have declined drastically since the second half of the 20th century (as in Azerbaijan) and in others this decline has accelerated more recently, mainly in southwestern Russia, Armenia, and in the coastal regions of Israel. The main threats to the eastern subspecies clades of *T. graeca* are the degradation and loss of habitats by urbanization and development, bush fires, and agricultural mechanization, while the legal collection for the international pet trade, especially to Europe, is currently much more regulated than in previous decades.

Distribution. – Southeastern Europe and southwestern Asia, including Bulgaria, Greece, Kosovo, North Macedonia, Romania, Russia, Serbia, Turkey (Türkiye), Armenia, Azerbaijan, Georgia, Iran, Iraq, Israel, Jordan, Lebanon, Palestine, and Syria.

Synonymy. – *Testudo graeca* Linnaeus 1758*, Testudo terrestris* Forskål 1775, *Testudo ecaudata* Pallas 1814, *Testudo ibera* Pallas 1814, *Testudo zarudnyi* Nikolsky 1896, *Testudo ibera bicaudalis* Venzmer 1920, *Testudo buxtoni* Boulenger 1921, *Testudo ibera racovitzai* Călinescu 1931*, Testudo floweri* Bodenheimer 1935*, Testudo graeca nikolskii* Chkhikvadze and Tuniev 1986*, Testudo graeca anamurensis* Weissinger 1987*, Testudo graeca armeniaca* Chkhikvadze and Bakradze 1991, *Testudo antakyensis* Perälä 1996*, Testudo graeca pallasi* Chkhikvadze and Bakradze 2002*, Testudo perses* Perälä 2002, *Testudo dagestanica* Chkhikvadze, Mazanaeva, and Shammakov 2011.

Subspecies . – Based on molecular analyses and some morphological traits, five subspecies are currently recognized among the eastern clades of the Spur-thighed Tortoise: *T. g. armeniaca*, Armenian Tortoise, Araxes Tortoise (Armenia, Azerbaijan, Iran, Russia [Dagestan], Turkey); *T. g. buxtoni*, Zagros Tortoise, Buxton's Tortoise (Iran, Iraq, Turkey); *T. g. ibera*, Anatolian Tortoise, Greek Tortoise, Asia Minor Tortoise (Bulgaria, Georgia, Greece, Kosovo, North Macedonia, Romania, Russia [Krasnodar], Serbia, Turkey); *T. g. terrestris*, Levantine Tortoise, Mesopotamian Tortoise (Israel, Jordan, Lebanon, Palestine, Syria, Turkey); and *T. g. zarudnyi*, Kerman Tortoise, Iranian Tortoise (Iran).

Status. – IUCN 2022 Red List: Vulnerable (VU A1cd, assessed 1996); Regional (Europe): Vulnerable (VU A2bcde+4bcde, assessed 2009); CITES: Appendix II, as Testudinidae spp.; EU: Annex A (regulation of trade of fauna and flora); Bern Convention: Annex II; Bulgaria: Endangered (EN A3ac); North Macedonia: Vulnerable; Greece: Least Concern; Iran: Vulnerable; Israel: Vulnerable (VU A1cd).

Taxonomy. — The Spur-thighed Tortoise, *Testudo graeca*, originally described by Linnaeus (1758), is a polytypic species currently comprising 10 subspecies based on morphological and genetic criteria (Fritz et al. 2007; TTWG 2021). The species inhabits a vast geographic region including southern Europe and some Mediterranean islands (e.g., Mallorca, Sardinia, Samos, Thassos), northern Africa, and southwestern Asia (Iverson 1992; Buskirk et al. 2001; Kuzmin 2002; Roll et al. 2017; Escoriza et al. 2022), and is separated into geographically-based genetic clades. The western clade (including northwestern Africa and south-western Europe) constitutes a genetically monophyletic group (Graciá et al. 2017). The eastern clades extend from the Balkans to southeastern Iran, with five mitochondrial DNA clusters identified, currently generally recognized as subspecies (Parham et al. 2006; Fritz et al. 2007; Graciá et al. 2017; Türkozan et al. 2018; Ranjbar et al. 2022): *T. g. armeniaca* Chkhikvadze and Bakradze 1991, *T. g. buxtoni*

Figure 1. Adult female Armenian Tortoise, *Testudo graeca armeniaca*, on the western shores of the Caspian Sea, Derbentsky District, Dagestan, Russia. Photo by Liudmila Mazanaeva.

Figure 2. Variability in the coloration of the eastern clades of *Testudo graeca*. *Left*: Anatolian Tortoise, *Testudo graeca ibera*, a dark individual from the Eastern Rhodopes Mountains, southern Bulgaria. Photo by Georgi Popgeorgiev. *Right*: Levantine Tortoise, *Testudo graeca terrestris*, a flavistic individual from the northern Negev, Israel. Photo by Alex Slavenko.

Boulenger 1921, *T. g. ibera* Pallas 1814, *T. g. terrestris* Forskål 1775, and *T. g. zarudnyi* Nikolsky 1896.

High genetic diversity exists in northeastern Anatolia, Armenia, and northern Iran (Arakelyan et al. 2018; Türkozan et al. 2018). The clade present in southeastern Iran (*T. g. zarudnyi*) is genetically well separated from the other eastern clades, having diverged from these ca. 6.7 mya ago, following the uplift of the Zagros mountains during the Pliocene (Ranjbar et al. 2022). However, syntopic occurrence of *T. g. ibera* and *T. g. terrestris* (Türkozan et al. 2018), *T. g. ibera* and *T. g. armeniaca* (Mashkaryan et al. 2013) and *T. g. armeniaca* and *T. g. buxtoni* (Javanbakht et al. 2017), extensive gene flow among mtDNA clades (Mashkaryan et al. 2013; Mikulícek et al. 2013), and hybrid zones in the Transcaucasus between some of these eastern clade genetic clusters (*ibera*, *armeniaca,* and *buxtoni*) (Mashkaryan et al. 2013) have been reported. Furthermore, recent morphologic comparisons of molecular clades do not reveal distinctive diagnostic characteristics for the identification of subspecies, e.g., the *armeniaca* mtDNA clade in Turkey includes a morphometrically distinct burrowing ecomorph, but individuals outside Turkey sometimes lack this distinctive *armeniaca* morphotype (Türkozan et al. 2018). We therefore use the term "subspecies clade" to describe these molecular clades (evolutionarily significant units) of *Testudo graeca* throughout the text.

Other subspecies have been described from among these eastern clades based on morphological characters, but they appear to be local forms (or perhaps ecotypes) that do not show sufficient divergence in their mitochondrial DNA (Fritz et al. 2007; Parham et al. 2006, 2012; Türkozan et al. 2018) to warrant subspecific status.

Following mtDNA evidence, the subspecies *T. g. pallasi* Chkhikvadze and Bakradze 2002 is a subjective synonym of *T. g. armeniaca*; *T. g. racovitzai* Călinescu 1931 and *T. g. nikolskii* Chkhikvadze and Tuniyev 1986 are subjective

Figure 3. Adult male Anatolian Tortoise, *Testudo graeca ibera*, from Dadia forest, northeastern Greece. Photos by Elias Tzoras.

Figure 4. Adult female Anatolian Tortoise, *Testudo graeca ibera*, from Loutros, northeastern Greece. Photo by Elias Tzoras.

Figure 5. Juvenile Anatolian Tortoise, *Testudo graeca ibera,* from Proskinites, northeastern Greece. Photo by Elias Tzoras.

Figure 6. Adult Levantine Tortoise, *Testudo graeca terrestris* (*anamurensis* form), from southern Turkey. Note the elongated appearance and marginal flaring reminiscent of *Testudo marginata*. Photo by Oguz Türkozan.

Figure 7. Adult Armenian Tortoise, *Testudo graeca armeniaca*, from Aralik, eastern Turkey. Photo by Oguz Türkozan.

synonyms of *T. g. ibera*; *T. ibera bicaudalis* Venzmer 1920, *Testudo floweri* Bodenheimer 1935, *Testudo antakyensis* Perälä 1996, and *T. g. anamurensis* Weissinger 1987 are subjective synonyms of *T. g. terrestris*; and *T. g. perses* Perälä 2002 is a subjective synonym of *T. g. buxtoni*. See TTWG (2021) for a full synonymy of the eastern subspecies of *T. graeca,* including several *nomina nuda*.

Description. —The eastern clades of *T. graeca* include small to medium-sized tortoises (usually adult individuals range between 12–30 cm midline SCL), although some males occasionally reach larger maximum sizes (up to 35.8 cm midline SCL, or 38.9 cm maximum SCL, and occasionally possibly up to 46.0 cm), larger than those in the western clade (Highfield and Martin 1989; Beshkov 1997; Türkozan et al. 2004b; Escoriza et al. 2022).

On average, adult females are generally slightly larger and heavier than males in most eastern clade regions or populations; although in approximately 30% of surveyed populations across the range, as documented below, males reach a similar or larger average and/or maximum size, including the largest individuals known. Female mean midline SCLs in eastern subspecies clades range from 14.5–21.9 cm per region or population (mean 19.7 cm, *n* = 1274) and male mean midline SCLs range from 13.5–24.1 cm (mean 18.6 cm, *n* = 1677) (Table 1). Females have mean body mass ranging from ca. 700–2240 g (average 1630 g, maximum 3225 g); males have mean body mass ranging from ca. 420–2700 g (average 1560 g, maximum 7000 g). Body size may be correlated with latitude in some populations of the eastern clades (Werner et al. 2016).

In the eastern clades, two extreme phenotypes (a flattened carapace without a hinge in the plastron vs. a high-domed carapace with a slightly hinged plastron) and a range of intermediate forms are not associated with genetic divergence (Pieh et al. 2002; Arakelyan et al. 2018).

The first phenotype corresponds to a burrowing steppe ecotype, characterized by a flattened carapacial appearance in lateral profile and oval from above, resembling the morphology of *Agrionemys horsfieldii* (Berglas 2000). The second phenotype corresponds to a non-burrowing mesic Mediterranean ecotype, with a domed carapace, raised in lateral profile and trapezoidal from above, with a movable xiphiplastron (Pieh et al. 2002).

However, in Dagestan, Russia, all individuals, regardless of the shape of the carapace (flattened or domed), have a movable xiphiplastron (U.A. Gichikhanova, pers. comm.). Moreover, in some regions, such as Dagestan, both phenotypes are found at the same localities, e.g., on clay-stony soils, as well as on sandy and semi-sandy soils (Mazanaeva, unpubl. data). An important phenotypic plasticity has also been observed in the Zagros Mountains of Iran, demonstrating morphological convergence between the two subspecies present in this region (*T. g. buxtoni* and *T. g. zarudnyi*) when they occupy environmentally similar areas (Ranjbar et al. 2022).

Carapace coloration is variable, from uniformly dark individuals (typically in the burrowing phenotype, but not exclusively) to ones with a contrasting pattern on a light background and black spots on the marginals, costals and vertebral scutes. This color pattern is very similar to that of the western clade of *T. graeca*, although the pattern may be darker with less pronounced spots, and consists of a lighter background (golden yellow, orange to brown-mustard) with the scutes edged with black, surrounding or connecting with a central dark spot. The plastron may be uniformly dark, but typically has a light background pattern with elongated black spots parallel to the longitudinal axis, which may be more or less symmetrical and form two nearly continuous bands. Juveniles have a similar color pattern to adults, although they are usually lighter (Auer and Herz 2021).

The carapace typically consists of 5 vertebral, 4 pairs of costal (pleural) scutes and 11 pairs of marginal scutes, plus one nuchal and one undivided supracaudal scute. The plastron comprises 6 pairs of scutes, including broad abdominals, moderately sized gulars and femorals, and

Figure 8. Iranian *Testudo graeca*. *Left*: Zagros Tortoise, *Testudo graeca buxtoni*, Kordestan, Iran. *Right*: Kerman Tortoises, *Testudo graeca zarudnyi*, mating, Kerman, Iran. Photos by Hossein Javanbakht.

relatively narrow humerals. Posterior marginal scutes may be markedly flared. *Testudo graeca* typically has one small conical keratinous spur on each thigh, absent in other broadly sympatric tortoises (except in some individuals of *T. marginata*; Bour 1995).

The head is rounded and usually almost uniformly dark, with lighter edges on the cephalic scales. Forms with partially or almost entirely yellow heads (previously recognized as the subspecies *antakyensis* and *floweri*) occur along the coast of southeastern Turkey, Lebanon, and Israel. The forelimbs have large and imbricate cuspidal scales in 3–6 longitudinal series and five claws; hindlimbs have four claws. The limbs may have light background color, with scattered darker scales or completely dark. Males are generally smaller than females, with proportionately longer tails, a shorter, concave plastron, and a slightly incurved supracaudal scute (Weissinger 1987; Chkhikvadze and Bakradze 1991; Perälä 2002).

Testudo graeca armeniaca. — This subspecies clade, referred to as the Armenian Tortoise or Araxes Tortoise, is characterized by its dorso-ventrally flattened carapace (height less than 50% of the SCL; Pieh et al. 2002), distinctly marked grooves separating costal, vertebral, and marginal scutes, posterior marginals slightly flared, and its general coloration, which can be uniformly dark, including the plastron, head, and limbs. However, this subspecies clade has high morphological variability along its distribution range, and the Turkish populations show a remarkably low domed carapace in comparison to others (Arakelyan et al. 2018). The intensity of color tones changes with age and does not depend on the biotope. The color tone of the scales on the head, limbs and tail corresponds to that of the carapace (Mazanaeva, unpubl. data). The tail is thick and has a blunt tip. Hatchlings have the first marginals folded inward (Pieh et al. 2002).

In northeastern Turkey, near the Armenian border, males have an average SCL = 17.1 cm ± 1.0 SD (range 15.2–18.7 cm) and females 19.2 cm ± 1.9 SD (range 14.7–22.0 cm) (n = 26) (Türkozan et al. 2010). In Armenia, males have an average SCL of 18.3 cm ± 0.6 SD (range 16.5–19.8 cm) and females 20.0 cm ± 0.4 SD (range 18.1–21.8 cm) (Arakelyan et al. 2011). In Dagestan (southwestern Russia), males have an average SCL of 18.7 cm ± 1.0 SD (range 15.2–21.0 cm, n = 33), and females 21.2 cm ± 1.2 SD (range 11.3–24.9 cm, n = 60) (Gichikhanova et al. 2019); the largest individuals were females with SCL = 24.7 cm and 24.9 cm (Ckhikvadze and Bakradze 2002; Gichikhanova et al. 2019). In northern Iran, males average slightly larger than females, with male mean SCL = 21.5 cm and female mean SCL = 20.8 cm (Javanbakht, unpubl. data). The skull of this subspecies has a strong posterior emargination of the maxillary surfaces (Pieh et al. 2002).

Testudo graeca buxtoni. — This subspecies clade, referred to as the Zagros Tortoise or Buxton's Tortoise, has a carapace that is rectangular when seen from above and trapezoidal in lateral profile, relatively domed and with slightly flared anterior and posterior marginals in males (Schmidt 1939). Males have a higher carapace than females (Rezazadeh et al. 2014). The coloration is chocolate brown or orange, with diffuse and inconspicuous black spots. The head and limbs are uniformly dark. The plastron is kinetic and usually shows a dark and uniform pattern, but with lighter scute boundaries (Türkozan et al. 2004a). Hatchlings are lighter colored, having a straw-yellow ground color, with the edges of the dorsal plates edged with brown, a pale plastron, with some irregular black spots, and yellowish head and limbs (Sadeghi and Torki 2012).

In Turkey, males have an average SCL = 19.5 cm ± 1.1 SD (range 17.9–20.5 cm) and females 21.4 cm ± 3.8 SD (range 17.9–27.3 cm) (n = 13) (Türkozan et al. 2010). In

Figure 9. Adult female Anatolian Tortoise, *Testudo graeca ibera*, Bulgaria. Photo by Georgi Popgeorgiev.

Figure 10. Hatchling Levantine Tortoise, *Testudo graeca terrestris*, Haifa, Israel. Photo by Uri Shanas.

Iran, males reach an SCL of 30.0 cm and females 28.7 cm (n = 114), and are slightly larger on average than females (22.0 cm SCL vs. 21.7 cm) (Javanbakht, unpubl. data). Rezazadeh et al. (2014) reported a higher average SCL in males than in females in Ardabil province, northwestern Iran, with a mean SCL of 22.3 cm (range 15.1–46.0 cm, n = 20) in males and 17.1 cm (range 12.0–30.0 cm, n = 12) in females; the exceptionally large male reported as having an SCL of 46 cm is an apparent record for the eastern subspecies clades, but might possibly be in error.

Testudo graeca ibera. — This subspecies clade, referred to as the Anatolian Tortoise or Greek Tortoise or Asia Minor Tortoise, has highly variable morphology, frequently with a domed carapace, with maximum central convexity, but some have a more rectangular appearance. Vertebral scutes are wider than long, locally variable in number and form, particularly the second and third (Kuzmin 2002). Some males have long, flared posterior marginals. Some specimens may also have anomalies in the plastral scutes, with additional small-sized scutes (Stojanov 2000). The shell coloration is variable and without a clear geographic pattern: almost uniformly black carapaces (e.g., Samothraki Island; Clark 1991) or with a light background, mustard brown or greenish yellow, with radial dark spots on the costal, vertebral, and marginal scutes.

In northern Greece, the mean SCL in a study of 930 *T. g. ibera* was 17.8 cm for males and 19.5 cm for females, with a mean body mass of 1164 g for males and 1578 g for females (Willemsen and Hailey 2003). In the Evros district of northeastern Greece, males had an average SCL of 19.2 cm ± 1.7 SD and females 21.4 cm ± 2.1 SD; males had an average body mass of 1558 g ± 378 SD and females an average body mass of 2091 g ± 533 SD (Makridou et al. 2019). On Thassos, the maximum SCL of males was 21.0 cm and of females 24.5 cm (Cattaneo 2001). On Samothraki (northern Aegean) Buttle (1989) reported an unsexed specimen of 28.0 cm. On Symi (Dodecanese, southern Aegean), the maximum SCL was 30.0 cm (Wilson and Grillitsch 2009).

In southwestern Turkey (Izmir), males had an average SCL of 18.7 cm ± 2.8 SD (range 16.0–24.2 cm) and females 18.7 cm ± 1.2 SD (range 17.2–20.5 cm) (n = 16) (Türkozan et al. 2005). In central Turkey (Nevşehir, Cappadocia) females had an average SCL of 20.7 cm ± 0.5 SD (range 18.7–24.0 cm) and an average body mass of 1863 ± 505 g (range 1340–2601 g; Akveran and Ayas 2019).

The geographically isolated subpopulation in Krasnodar, on the northeast Russian coast of the Black Sea (*nikolskii* form), tends to have a relatively higher carapace with a medial keel on the vertebral scutes with predominantly dark-colored individuals (69–77% of the specimens; Chkhikvadze and Tuniyev 1986), with a series of four rounded scales on the forelimbs, and some have the claws of the forelimbs lightly colored: yellow (20–30%) or gray (16–27%) (Leontyeva et al. 2001). Females are slightly larger than males, with mean SCL of males 19.2 cm (maximum 29.4 cm, n = 195) and mean SCL for females 20.0 cm (maximum 29.7 cm, n = 182) (Leontyeva et al. 2001).

In eastern Georgia, the mean SCL of males was 17.9 cm (range 15.2–19.8 cm) and that of females was 21.0 cm (range 15.0–25.0 cm) (Auer and Herz 2021), with a maximum SCL of 26.0 cm (Muskhelishvili 1970).

In northeastern Romania, average SCL of males was 20.1 cm, with a maximum SCL of 30.1 cm, and average body mass was 1718 g, with a maximum of 4885 g (Cogălniceanu et al. 2010). Two record-sized males from Bulgaria reached midline SCLs of 33.5 cm and 35.8 cm (maximum SCLs of 36.4 and 38.9 cm), the latter with a mass of 7000 g after feeding (Beshkov 1997). However, based on recent data from across Bulgaria, the maximum midline SCLs measured were 24.7 cm for a male (n = 723) and 25.8 cm for a female (n = 419) (Popgeorgiev and Kornilev, unpubl. data).

Testudo graeca terrestris. — This subspecies clade, referred to as the Levantine Tortoise or Mesopotamian Tortoise, is another morphologically highly variable taxon, with other synonymized geographic forms (*anamurensis*, *antakyensis*, and *floweri*). These differ in the shape of the carapace, with regularly convex forms (*antakyensis, floweri, terrestris*) or with a flattened and rectangular carapace with broad and serrated posterior marginals (*anamurensis*) resembling *T. marginata* (Perälä 2001). Coloration may be uniformly dark or mustard/light greenish-yellow edged with black spots, but there are forms with black spots reduced to dots, with narrow lines on the marginal, vertebral, and costal scutes, or even almost completely absent, as in the regions of Wadi Gaza and Haifa, Jerusalem, and the northern Negev (Hoofien *in* Bringsøe and Buskirk 1998; Rabou et al. 2007). These individuals also have less sculptured carapace scutes (Sivan and Werner 1992).

In yellow flavistic forms, the carapace of adults tends to have a lighter pattern than juveniles (age-induced flavism) (Bringsøe and Buskirk 1998). However, mixed with these flavistic individuals are others with a darker pattern, having dark markings on the costal, vertebral, and marginal scutes, although maintaining a partially yellow head (Rabou et al. 2007). Individuals with partially or almost completely yellow heads are dominant in Iskenderun, Turkey (*antakyensis*), and in Jordan and southern and coastal Israel (*floweri*) (Herrn 1966; Disi et al. 2001; Werner 2016).

The thigh spurs can be curved inwards and have sharply pointed tips in some specimens (e.g., in Mardin and Adiyaman, southern Turkey; Türkozan et al. 2003). Claws are gray or black (Perälä and Bour 2004). The plastral pattern usually shows asymmetrical or radiating black spots on a light background, with a symmetrical distribution about a medial axis. However, in some indi-

Table 1. Summary of straightline midline carapace length (SCL) measurements (mean, maximum, and sample size) as documented for various populations and regions across the range of the eastern subspecies clades of *Testudo graeca*. Weighted average of mean SCLs calculated as the total sum of (*n* * mean) per sex per documented population or region (*n* = 19, marked with *), divided by the total sample size per sex (*n* = 1677 males, 1274 females).

		Male SCL			**Female SCL**			**Sexes Combined**		
Subspecies Clade and Population	**Total *n***	**Mean**	**Max**	***n***	**Mean**	**Max**	***n***	**Mean**	**Max**	**Source**
T. g. armeniaca										
northeastern Turkey *	26	17.1	18.7	15	19.2	22.0	11	18.0	22.0	Türkozan et al. 2010
Armenia		18.3	19.8		20.0	21.8			21.8	Arakelyan et al. 2011
Dagestan, Russia *	93	18.7	21.0	33	21.2	24.9	60	20.3	24.9	Gichikhanova et al. 2019
northern Iran *	21	21.5	24.9	11	20.8	27.1	10	21.2	27.1	Javanbakht, unpubl. data
T. g. buxtoni										
eastern Turkey *	13	19.5	20.5	8	21.4	27.3	5	20.2	27.3	Türkozan et al. 2010
western and southern Iran *	114	22.0	30.0	64	21.7	28.7	50	21.9	30.0	Javanbakht, unpubl. data
Ardabil, northern Iran *	32	22.3	46.0	20	17.1	30.0	12	20.3	46.0	Rezazadeh et al. 2014
T. g. ibera										
northern Greece	930	17.8	25.0		19.5	26.0			26.0	Willemsen and Hailey 2003
Evros, northeastern Greece *	113	19.2		36	21.4		77	20.7		Makridou et al. 2019
Thassos Isl., Greece	58		21.0			24.5			24.5	Cattaneo 2001
Samothraki Isl., Greece									28.0	Buttle 1989
Symi Isl., Greece									30.0	Wilson and Grillitsch 2009
Izmir, southwestern Turkey *	16	18.7	24.2	7	18.7	20.5	9	18.7	24.2	Türkozan et al. 2005
western and central Turkey *	521	18.4	26.5	257	19.9	26.9	264	19.2	26.9	Türkozan et al. 2010
Cappadocia, central Turkey	9				20.7	24.0	9		24.0	Akveran and Ayas 2019
eastern Georgia		17.9	19.8		21.0	25.0			25.0	Auer and Herz 2021
eastern Georgia						26.0			26.0	Muskhelishvili 1970
northeastern Romania	101	20.1	30.1						30.1	Cogălniceanu et al. 2010
Bulgaria			35.8						35.8	Beshkov 1997
Bulgaria *	1142	16.8	24.7	723	18.5	25.8	419	17.4	25.8	Popgeorgiev and Kornilev, unpubl. data
Krasnodar, Russia *	377	19.2	29.4	195	20.0	29.7	182	19.6	29.7	Leontyeva et al. 2001
T. g. terrestris										
Anamur, Turkey *	51	19.3	23.5	30	21.2	26.0	21	20.1	26.0	Türkozan et al. 2010
Antakya, Turkey *	16	13.8	15.5	8	14.5	18.8	8	14.1	18.8	Türkozan et al. 2010
Lake Van (Se), east Turkey *	199	23.0	26.7	137	20.8	24.6	62	22.3	26.7	Crucitti and Emiliani 2012
Lake Van (La), east Turkey *	76	24.1	28.0	53	21.9	30.8	23	23.4	30.8	Crucitti and Emiliani 2012
Mardin, southeastern Turkey *	24	20.4	23.9	16	20.9	23.8	8	20.5	23.9	Türkozan et al. 2003, 2005
southern Jordan	7		11.7			15.6			15.6	Gasperetti et al. 1993
Israel		13.6			16.6				16.6	Bernheim 2014
Israel *	25	13.5	14.8	8	15.7	21.7	17	15.0	21.7	Meiri, unpubl. data
Taurus Mts, southern Turkey *	65	20.4	27.4	40	23.6	29.5	25	21.6	29.5	Türkozan et al. 2004b
T. g. zarudnyi										
eastern Iran						28.2			28.2	Highfield and Martin 1989
eastern Iran *	27	20.2	24.7	16	18.7	24.1	11	19.6	24.7	Javanbakht, unpubl. data
Weighted Average of Mean SCLs		**18.6**		1677	**19.7**		1274			

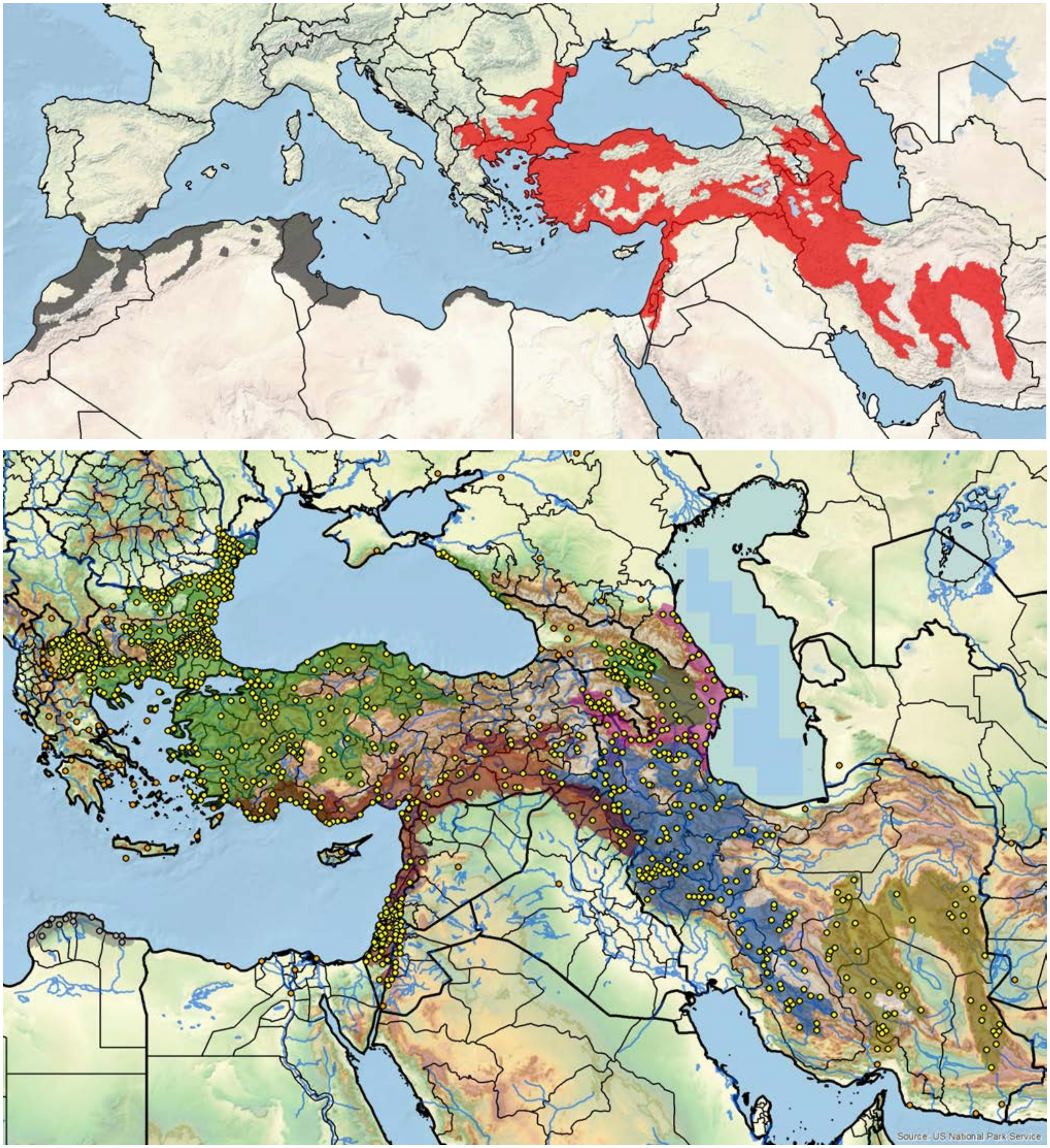

Figure 11a. *Top*: Outline map of total *Testudo graeca* estimated historical indigenous distribution; gray = western subspecies clade (see TTWG 2021 and Escoriza et al. 2022); red = eastern subspecies clades (see below). *Bottom*: Overall distribution of the eastern subspecies clades of *Testudo graeca* in southeastern Europe and southwestern Asia. Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992), other more recent literature records (see TTWG 2017, 2021), and authors' additional data; orange dots = introduced or possibly historically relict populations or individual trade or translocated specimens; gray dots and gray shading = eastern extent of the western subspecies clade of *T. graeca* (= *T. g. cyrenaica*); colored shading = estimated historical indigenous ranges of: 1) *T. g. armeniaca* = purple; 2) *T. g. buxtoni* = blue; 3) *T. g. ibera* = green; 4) *T. g. terrestris* = brown; and 5) *T. g. zarudnyi* = olive; colored shading overlap areas = hybridization zones and intergrades (*armeniaca–ibera*, *armeniaca–buxtoni, ibera–terrestris,* and *buxtoni–terrestris*). Distribution based on fine-scaled GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs based on Buhlmann et al. (2009), TTWG (2017, 2021), and data from authors and other sources.

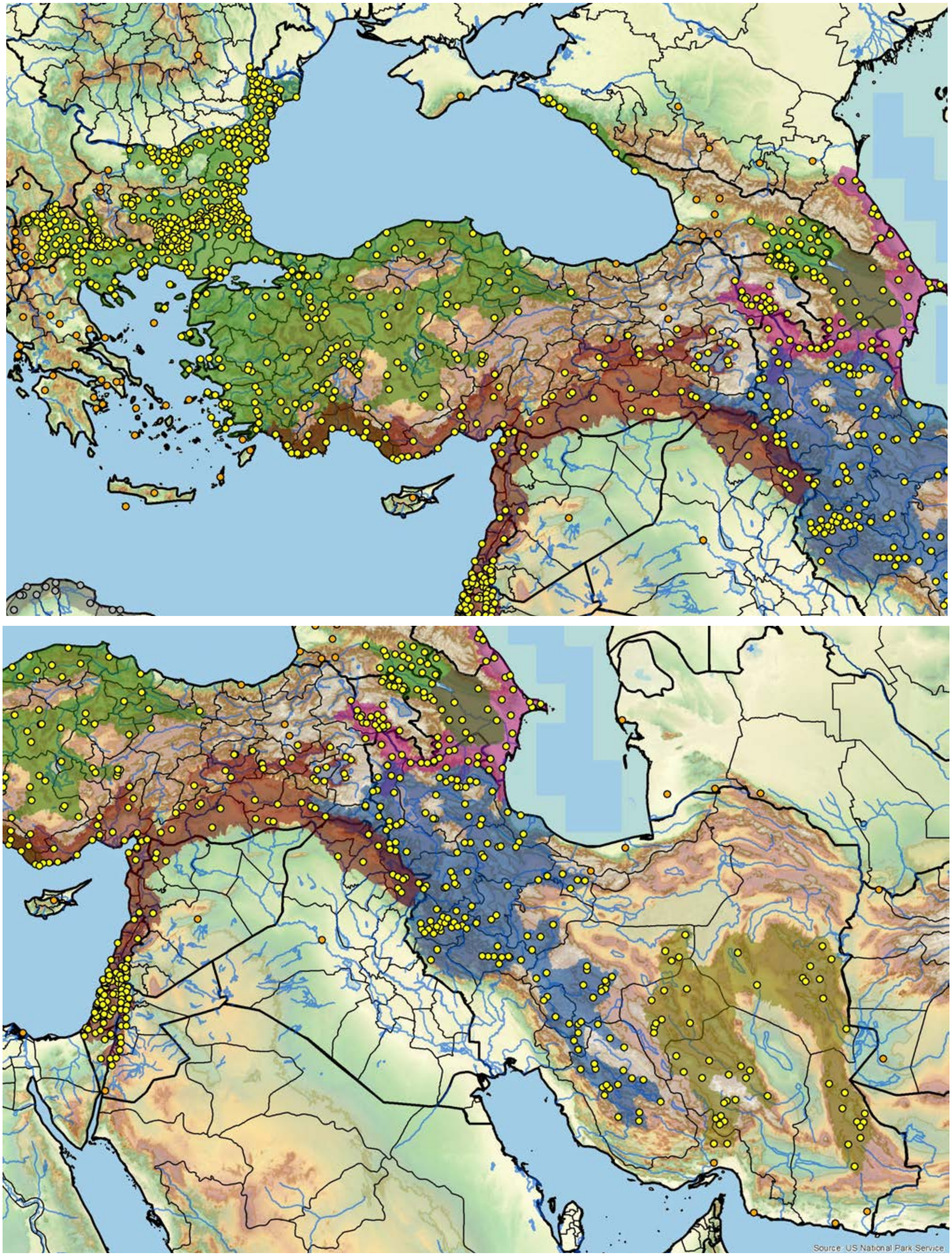

Figure 11b. *Top*: Enlarged view of the northwestern distribution of the eastern subspecies clades of *Testudo graeca*. *Bottom*: Enlarged view of the southeastern distribution of the eastern subspecies clades of *Testudo graeca*. Legend for dots and color shadings as in Figure 11a.

viduals the coloration is darker, a diffuse chestnut brown, with small lighter patches.

Size may also vary geographically, and individuals from the Gulf of Iskenderun in Turkey (*antakyensis* form), southern Israel (*floweri* form) and southern Jordan are smaller (Sivan and Werner 1992; Gasperetti et al. 1993; Türkozan et al. 2010).

In Alanya-Anamur, Turkey (*anamurensis* form), males have an average SCL of 19.3 cm ± 2.4 SD (range 12.3–23.5 cm) and females average SCL = 21.2 cm ± 3.6 (range 12.3–26.0 cm) (n = 51) (Türkozan et al. 2010). For this same form, Highfield (1990a) reported males with SCL of 21.8 cm, 22.0 cm (body mass = 2200 g), 23.0 cm, and 23.5 cm, and one female of 21.8 cm.

Males of the *antakyensis* form from Çaylı-Dörty and Antakya, Turkey, have a mean SCL of 13.8 cm ± 1.9 SD (range 10.8–15.5 cm) and females a mean SCL of 14.5 cm ± 3.2 (range 10.0–18.8 cm) (n = 16) (Türkozan et al. 2010). In two localities in eastern Turkey (the surroundings of Lake Van) males had an average SCL of 23.0–24.1 cm (range 17.7–28.0 cm) and females 20.8–21.9 cm (range 13.5–30.8 cm); males had an average body mass of 2474–2708 g (maximum 3610 g) and females an average body mass of 2016–2239 g (maximum 3225 g) (Crucitti and Emiliani 2012). In southeastern Turkey (Mardin), males have a mean SCL of 20.4 cm ± 2.3 SD (range 13.5–23.9 cm) and females a mean SCL of 20.9 cm ± 2.4 SD (range 15.5–23.8 cm) (n = 24) (Türkozan et al. 2003).

In southern Jordan, males have an SCL of 9.8–11.7 cm and females 10.1–15.6 cm (Gasperetti et al. 1993). In Israel, both mean SCL and mean mass were significantly higher in females than males (adult females mean SCL = 16.6 cm ± 0.35 SD; adult males mean SCL = 13.6 cm ± 0.28 SD; adult females mean mass = 885.2 g ± 33.76 SD; adult males mean mass = 477.4 g ± 20.22 SD) (Bernheim 2014). In Mount Carmel and Golan Heights, SCL reached 16.0 cm in males and 21.0 cm in females (Meiri et al. 2011; Bar et al. 2021), with body masses of 250–420 g in males and 540–840 g in females (Werner 2016). In a sample of individuals collected throughout Israel, average adult SCL was 13.5 cm in males and 15.7 cm in females and the average adult male body mass was 422 (range 257–752 g) vs. 700 (range 253–1812 g) in adult females (Meiri, unpubl. data). In Israel, the size of tortoises decreases latitudinally, from the Golan Heights to the Negev (Bar et al. 2021). In the northern Negev, carapace lengths of 12.5–16.3 cm were reported for three females (Bringsøe and Buskirk 1998).

The maximum SCL of *T. g. terrestris* was 29.5 cm in the Western Taurus mountains of southern Turkey (Türkozan et al. 2004b) and 30.8 cm in the Nemrut Dağı of eastern Turkey (Crucitti and Emiliani 2012).

Testudo graeca zarudnyi. — This subspecies clade, referred to as the Kerman Tortoise or Iranian Tortoise, has an elongated and convex carapace, with flared and serrated posterior marginals, resembling *T. marginata* and the *anamurensis* form of *T. g. terrestris* (Mertens 1946; Perälä 2001). The tail is relatively thin and pointed at the tip (Pieh et al. 2002). The carapace is orange to chestnut brown with slightly marked dark spots, sometimes with olive greenish tinges (Pieh et al. 2002). Marginal scute edges show translucent yellow horn tips (Highfield and Martin 1989). The plastron is yellow or dark brown, with darker but inconspicuous spots.

Females reach an SCL of 28.2 cm with body mass of 3700 g (Highfield and Martin 1989). In southeastern Iran, males reach 24.7 cm and 2450 g and females reach 24.1 cm and 2700 g (Javanbakht, unpubl. data).

Distribution. — The eastern clades of *T. graeca* are almost continuously distributed in southeastern Europe and southwestern Asia. The current westernmost native populations are found in southern Serbia and North Macedonia, while the eastern edge of the range is located in southeastern Iran (Kuh-e Taftan; Javanbakht et al. 2017), close to the Pakistan border.

The species is not present in Croatia, and recent alleged records from there (Dieckmann 2004) are possibly of *Testudo hermanni boettgeri* (Tóth et al. 2006).

In Albania there is a record of *T. g. ibera* in the surroundings of Prespa Lake (Haxhiu 1998), but its presence has not been confirmed in recent surveys (Mizsei et al. 2017), so this species could either have been introduced in Albania (e.g., a released captive) or possibly extirpated, if previously native.

In Serbia and Kosovo, there is a tiny population of *T. g. ibera*, a continuation of the one occurring in North Macedonia (Arsovski and Sterijovski 2019). The species occurs only in the extreme south, in Preševo valley and the Starac and Šar Planina mountains, at 370–600 m; a record from Mitrovica, Kosovo, is likely a non-native translocation (Tomović et al. 2014, 2019).

In North Macedonia, *T. g. ibera* occurs mainly along the Strumica and Vardar valleys: Skopje, Štip, Katlanovo, Kalkovo, Gevgelija (Karaman 1928) and scattered in other parts of the country, although being less abundant than *T. hermanni* (Sterijovski et al. 2014; Uhrin et al. 2016; Arsovski and Sterijovski 2019). The species occurs at low elevations (155–211 m) in North Macedonia (Uhrin et al. 2016).

In Greece, *T. g. ibera* is distributed in the northeast continental part of the country, between the wetland of Lake Alyki (west of Thessaloniki) and eastwards to the regions of Macedonia and Thrace (Stubbs et al. 1981; Crucciti and Tringali 1986; Dimitropoulos 1988; Petrov 2004; Georgiev and Mollov 2016; Makridou et al. 2019). It has also been reported from many Aegean islands: Chios, Kalymnos, Kos, Lemnos, Leros, Lesbos, Samos, Samothraki, Symi, and Thasos (Watson 1962; Clark 1991, 1999; Schneider

1986; Buttle 1989, 1990, 1995; Broggi 1994, 1997a, 2002; Müller 1995; Kasapidis et al. 1996; Cattaneo 2001, 2003, 2005), and in Agios Efstratios, Crete, Gavdos, Ikaria, Karpathos, Kythnos, Milos, Mykonos, Rhodes, Salamina (Salamis), Sesklia islet, and Skiathos, where it has probably been introduced (Ondrias 1968; Bringsøe 1986; Broggi 1997b, 2014; Cattaneo 1997; Valakos et al. 2008; Bader et al. 2009; Strachinis and Roussos 2016; Cattaneo et al. 2020). On Corfu and Lefkada (Ionian Sea) this species is not naturally present (Tóth et al. 2002), although reported as such by Werner (1930). The records on Poros and Spetses (Spetsai) islands in the Argo-Saronic Gulf of Greece (Clark 1967) are misidentified specimens of *Testudo marginata* (Clark 1989). There are also some isolated records in other parts of central Greece and northern Peloponnese (Bringsøe 1986; Dimitropoulos and Gaethlich 1986; Valakos et al. 2008) that possibly do not represent established native populations. In Attica (southern mainland Greece), three individuals (possibly translocated) were recently reported (Annousis et al. 2021), while records from the beginning of the 20th century (Fiedler *in* Werner 1930) were attributed to *Testudo marginata* (Werner 1930).

In Bulgaria, *T. g. ibera* occurs throughout the country except for the northwest, where single individuals may be translocated by humans; in the southwestern mountains it has been found up to 1300 m (Beshkov 1984, 2015; Beshkov and Nanev 2006).

In Romania, *T. g. ibera* occurs widely throughout the lowlands and Black Sea coast: Ostrov, Oltina, Rasova, Hîrşova, reaching its northern limit in the Northern Dobrogean plateau: Cerna, Măcin Mountains (Funh and Vancea 1961; Cogălniceanu et al. 2010; Moraru et al. 2016) and locally in the Danube Delta: Cape Tasburum, Heraclea, Chituc, and Cetatea Histria (Török 2012).

In Turkey, this species extends over most of the country, except in the extreme northeast, between Samsun and the Georgian border (Bird 1936; Clark and Clark 1973; Kasparek 1990; Mulder 1995, 2019; Türkozan et al. 2010; Cihan and Tok 2014; Yildiz 2020). The distribution of *T. g. ibera* includes European Turkey, western and central Anatolia, and extends along the western Black Sea coasts. The easternmost record from the Black Sea region is from Samsun Province. The Çarşamba River probably limits the further eastern distribution along the eastern Black Sea coast (Türkozan et al. 2010, 2018). The northernmost Turkish population is recorded at Suşehri, Sivas Province. The steep Black Sea coastal habitats are not suitable for *T. graeca*.

The distribution of *T. g. terrestris* occurs along the Mediterranean coast of Turkey with Kızılağaç Village, Province Muğla as the westernmost distribution range and extends to Sağlarca Village near Province Eruh in the east. The northernmost distribution range of *T. g. terrestris* is limited by the Taurus Mountains range, except for an occurrence in Karapınar, central Anatolia, where *ibera* and *terrestris* occur syntopically. The distribution of *T. g. buxtoni* includes Şırnak (40 km east of the easternmost distribution of *T. g. terrestris*). The northernmost distribution record is from Başkale in Turkey. The distribution of *T. g. armeniaca* is limited to the Araxes Valley in Turkey (Türkozan et al. 2010, 2018). *Testudo g. buxtoni* reaches elevations of 2500 m in Yüksekova (southeastern region) and *T. g. terrestris* up to 2200 m in Van (central-eastern region) (Hellmich 1969; Mulder 1995; Crucitti and Emiliani 2012).

In Cyprus, a few remains of tortoises have been found in archaeological sites, e.g., an immature *T. graeca* (Kition, 3300–3200 ya) and a plastron and several polished carapace fragments and an almost complete carapace (Kalopsidha, 3650–3575 ya) (Karageorghis and Demas 1985; Hadjisterkotis and Reese 1994). These finds do not allow us to conclusively determine that *T. graeca* was part of the native fauna of Cyprus, given that the remains may belong to individuals imported from the mainland. Relatively recent records of *T. graeca* (1981 and 1994) found on Cyprus correspond to isolated individuals likely released by pet owners, with no naturalized populations found on the island (Baier et al. 2013).

Previous records in Ukraine, e.g., Crimea, Ivano-Frankivsk, and Mariupol, were possibly translocations (Kuzmin 2002), but the original description of *T. g. ibera* by Pallas (1814) included reference to its occurrence both in the Caucasus and along the steep southern mountainous Black Sea coast of Crimea, not far from its present occurrence in coastal Krasnodar, Russia, possibly representing a subsequently extirpated native population. Records outside the Caucasus / Black Sea region in Russia (e.g., Rostovskaya and Volgográdskaya) were most likely translocations or errors (Kuzmin 2002). In Russia, *T. g. ibera* is confined to a narrow coastal strip of the Black Sea (Krasnodar region): Anapa, Abinsk, Abrau Peninsula, and Sochi (Leontyeva et al. 2001), reaching elevations of 400 m (Mazanaeva et al. 2009). The fossil record indicates that the presence of *T. graeca* in this region of the northeastern Black coast does not exceed 12,000 ya (Bölling-Allerød interstadial; Leontyeva and Demin 1995).

In Dagestan (Russia), *T. g. armeniaca* occurs in the coastal lowlands of the Caspian Sea (Primorskaya lowland) southeast of the city of Makhachkala to the mouth of the Samur River on the border with Azerbaijan, and in the adjacent foothills, including the Narat-Tyube ridge, extending northwest from Makhachkala. Its elevational range in Dagestan is between -28 to 800 m (Mazanaeva 2001, 2009, 2013, 2021; Mazanaeva and Gichikhanova 2018, 2019, 2020b, 2021).

In Georgia, *T. g. ibera* is distributed in isolation along its northern Black Sea coast, reaching the southern limit in Pitsunda (Bannikov et al. 1977). There are other isolated records near the Turkish border, in Kobuleti, but they may be translocations (Auer and Herz 2021). In the center-south region of Georgia, the species has been recorded from Gori, Tbilisi, Bolnisi, and eastwards to Vashlovani National Park, close to the border with Azerbaijan (Chkhikvadze 2009; Auer and Herz 2021), and reaches an altitude of 800–1000 m (Muskhelishvili 1970).

In Azerbaijan, the species is distributed throughout most of the country, including the Absheron Peninsula, reaching elevations up to 1500 m in Kelvaz (Bannikov et al. 1977; Alekperov 1978; Auer and Herz 2021).

In Armenia, *T. graeca* is distributed in the valley of the Araxes River and further north, in the provinces of Lori and Tavush (Zugmayer 1906; Arakelyan et al. 2011), and reaches an altitude of 1500 m, although in the north it does not exceed 950 m (Arakelyan and Parham 2008).

From Turkmenistan, there are a few records assumed to represent translocations, including a specimen from the Krasnowodsk region (eastern coast of the Caspian Sea), deposited in the collection of the Vienna Natural History Museum (NMW 19569). This specimen in appearance has some unique morphological features (Pieh and Perälä 2001). However, some of these features possibly correspond to an old individual, and it may not have been native to the region.

In Iran, *T. graeca* is widely distributed. In western Iran, including the Zagros Mountains, *T. g. buxtoni* occurs in the provinces of Gilan, Qazvin, Zanjan, Ardabil and West and East Azerbaijan, Tehran, Alborz, Markazi, Qom, Kordestan, Kermanshah, Kohgiluyeh Boyer-Ahmad, Fars, Esfahan, Chahar Mahaal, and Bakhtiari and Hamedan. In eastern Iran, *T. g. zarudnyi* occurs in the provinces of Sistan Va Baluchestan, Hormozgan, Kerman, Yazd, Khorasan Razavi, and South Khorasan (Parham et al. 2012; Safaei-Mahroo et al. 2015; Javanbakht et al. 2017). The subspecies *T. g. armeniaca* is only known in the northwest of Iran, in Jolfa (East Azerbaijan Province) (Javanbakht et al. 2017). The species reaches an altitude of 2500 m (Kharistan, Werner 1938) and 2615 m in Rabor (Kerman Province) (Javanbakht, unpubl. data), which represents the elevational record for the species. According to Pritchard (1966), this species is found mainly above 1500 m, but more recent surveys indicated that it is most common between 1000 and 2500 m (Javanbakht, unpubl. data).

In Iraq, *T. graeca* is only found in the north, at elevations between 525 and 1785 m (Reed and Marx 1959). The genetic affinities of these populations have not yet been clarified and they could belong to either Levantine *T. g. terrestris* or Zagrosian *T. g. buxtoni,* or be a contact zone between both taxa. We show them as *T. g. terrestris* on our map.

In Syria, *T. g. terrestris* occurs in the western coastal plains (Eiselt and Spitzenberger 1966), around Homs (Qattinah Lake; Boulenger 1923), Aleppo and Tartous (Schmidt 1939; Werner 1939), in Slanfah (Cedar Fir Reserve), and has also been recorded around Palmyra (Sindaco et al. 2006), although this last record was likely a translocated individual.

In Lebanon, *T. g. terrestris* occurs in the mountains near the Mediterranean coast: Nahr Ibrahim valley, Nahr El 'Assi, Shhim, Berqayel, Minyeh, Qornet Shewman, and Nabaa Al Safa (Hraoui Bloquet 1981; Hraoui Bloquet et al. 2002).

In Jordan, *T. g. terrestris* occurs in the northwest, between the border with Syria in the north and the mountains of Petra in the south (Gasperetti et al. 1993; Disi et al. 2001). There is a record in Al Aqabah (Gulf of Aqaba), in the extreme south, possibly a translocated individual (Gasperetti et al. 1993). *Testudo graeca* also was not recorded in recent surveys in other parts of the Gulf of Aqaba in Saudi Arabia (Aloufi and Amr 2015).

In Israel and Palestine regions, *T. g. terrestris* occurs throughout the Mediterranean biome, from Mt. Hermon, the Golan Heights and the Galilee mountains (Sivan and Werner 1992; Bar and Haimovitch 2011), the Carmel, coastal plain to the mountains of Samaria and Judea and as far south as the northern Negev, from the Hebron mountains in the east (northern Negev) westwards into Wadi Gaza (Tristram 1884; Buskirk 1967; Yom-Tov and Mendelssohn 1988; Rabou et al. 2007; Bar et al. 2021). It does not inhabit the Negev Desert in the south, except its northern fringes, nor the Judean Desert in the east. *Testudo graeca* is replaced by *Testudo kleinmanni* in the sandy regions of the western Negev and northern Egypt (Werner 1982; Buskirk 1996; Bar et al. 2021), although the two species are sympatric in at least one locality in the northern Negev (Be'er Mash'abim; Bringsøe and Buskirk 1998).

In Egypt, the presence of *T. graeca* was initially suggested by Anderson (1898) and later ruled out by Flower (1933). However, Wermuth and Mertens (1961) suggested its presence based on an individual acquired in a shop in Cairo and deposited in the Senckenberg Museum (Buskirk 1996). Later records are all from individuals acquired in shops (e.g. El Dabaa, northwestern Egypt (Lambert 1983), and therefore do not indicate native or naturalized populations occurring in Egypt (Buskirk 1996).

Habitat and Ecology. — In southeastern Europe and southwestern Asia, *T. graeca* occupies the Mediterranean, continental-Mediterranean, and cold to warm steppe belts, and locally the margins of subtropical deserts (BWh, BSk-BSh, Csa, Cfa, and Dsa types in the climatic classification of Köppen-Geiger, K–G; Peel et al. 2007), being replaced by *Agrionemys horsfieldii* and *Testudo kleinmanni* in more arid regions (Werner 2016; Escoriza and Ben Hassine 2022). Climatic conditions played a key role during the process of diversification of *T. graeca*, and the paleo-climate models

Figure 12. Adult Anatolian Tortoise, *Testudo graeca ibera,* in its habitat at Loutros, northeastern Greece. Photo by Elias Tzoras.

suggest that the different subspecies clades evolved in isolated refugium areas in the southern Mediterranean and southwestern Asia. Some of these subspecies clades occupy very distinct niches, which is particularly evident when comparing the current climate characteristics of the regions occupied by the eastern and western clades of *T. graeca* (Escoriza and Ben Hassine 2022).

The species shows a wide range of thermal tolerance. In Tulcea in northeast Romania (Cfa K–G type; *T. g. ibera*), the average air temperatures are -0.2°C in January and 24.3°C in July, with an accumulated annual precipitation of 524 mm. In Dagestan in Russia, in the habitats used by *T. g. armeniaca* in the coastal lowlands of the Caspian Sea (Primorskaya lowland), the average air temperatures are 1°C in January and 28°C in July, with an accumulated annual precipitation of 200 mm and an average annual temperature of 12.6°C. In the foothills in the same area, the average air temperatures are -1.0°C in January and 21.8°C in July, with an accumulated annual precipitation of 300–400 mm (Mazanaeva 2001, 2009, 2013, 2021; Mazanaeva and Gichikhanova 2018, 2019, 2020b, 2021). In Be'er Sheva in southern Israel (BWh K–G type; *T. g. terrestris*), the average air temperatures are 11.1°C in January and 26.3°C in July, with an accumulated annual precipitation of 132 mm. The average annual air temperature across the species' range is 14.8°C, with an accumulated annual precipitation of 416 mm (GARD database; Caetano et al. 2022).

In general, *T. graeca* tends to occupy open habitats, ranging from warm semi-deserts to alpine grasslands and agricultural lands, but also occurs at the margins of broad-leaf forests (e.g., in Serbia, Greece, southern Russia, and Armenia; Inozemtsev and Pereshkolnik 1994) and in open coniferous forests (e.g., in Jordan and Israel; Attum et al. 2011; Bar et al. 2021).

In Serbia, it appears at the margins of deciduous xerophytic oak forests, scrubland and dry grasslands (Tomović et al. 2019). In North Macedonia, *T. graeca* occupies open habitats, with small bushy formations, and urban parks, but is absent from dense forests (Arsovski and Sterijovski 2019).

In northeastern Greece, this species occupies open dry scrubland and spiny shrubland or *phrygana*, coastal heath, wetlands, as well as open coniferous woodlands (*Pinus brutia*) and the margins of deciduous oak forest (*Quercus cerris, Q. frainetto, Q. pubescens*) (Stubbs et al. 1981; Dimitropoulos 1988; Buttle 1989; Willemsen and Hailey 1989; Kati et al. 2007). In areas of sympatric contact with *T. hermanni*, the latter species prefers more forested habitats and has lower body temperatures (Wright et al. 1988). On Thasos Island *T. graeca ibera* occupies coastal dunes and heaths (Clark 1999; Cattaneo 2001). On the islands of Symi (southeastern Aegean), Lesvos and Samothraki (northern Aegean) this species appears in Mediterranean dry *prhygana* shrubland (Buttle 1995; Tsunis and Dimitropoulos 1994; Wilson and Grillitsch 2009).

In Bulgaria, *T. g. ibera* prefers open habitats (e.g., semi-steppe grassy areas, coastal sand dunes, sparse oak woodlands), while *T. hermanni* uses more heavily vegetated habitats; seasonally, *T. g. ibera* migrates from

Figure 13. Habitat of the Annatolian Tortoise, *Testudo graeca ibera,* in Marikostinovo village, southwestern Bulgaria. Photo by Georgi Popgeorgiev.

Figure 14. Habitat of the Armenian Tortoise, *Testudo graeca armeniaca,* in Narat-Tyube Ridge and Sarykum dune, Dagestan, Russia. Photo by Liudmila Mazanaeva.

open, dry and sandy areas to valleys with preserved foliage during summer heat and droughts (Petrov et al. 2004). In southeastern Bulgaria (Eastern Rhodopes), *T. g. ibera* and *T. hermanni boettgeri* occur sympatrically in open deciduous forests formed by oaks (*Quercus cerris, Q. frainetto*), ashes (*Fraxinus ornus)* and hornbeams (*Carpinus orientalis)*, bushes such as Cornelian cherries (*Cornus mas*) and Christ's thorns (*Paliurus spina-christi*), and tall grasses (30–40 cm) (Popgeorgiev 2008). In the Eastern Rhodopes, *T. g. ibera* populations are more abundant below 600 m and relatively scarce between 600 and 1300 m (Petrov 2004, 2007).

In the eastern coastal plains of Romania, *T. g. ibera* occurs in semi-steppe formations, scrubland, and agricultural lands (Moraru et al. 2016). Along the northern extent of its range, in Dobrogea, it occupies mixed habitats, composed of scattered trees (oaks and hornbeams) and bushes (*Cornus mas*, *Crataegus monogyna,* and *Rosa canina*) and patches of permanent grasses (*Stipa*) (Iftime and Iftime 2012).

In European Turkey, *T. g. ibera* occurs sympatrically with *T. hermanni boettgeri* in some areas, but the former prefers more open shrubland (Türkozan et al. 2019). In its Anatolian distribution range, *T. graeca* occurs in a wide variety of habitats, but more frequently associated with sclerophyllous vegetation. Depending on the season, tortoises were observed resting under thorny burnets (*Sarcopoterium)* or found near marshes under rushes (*Juncus)* (Arslan et al. 2021). Along the southern Turkey coast, the *anamurensis* form occurs in coastal dunes and associated scrubland (Perälä 1996; Taskavak and Türkozan 2004a). The *antakyensis* form occupies agricultural lands (vineyards) and open forests on low hills (400–500 m) (Taskavak and Türkozan 2004b). In eastern Anatolia, *T. g. armeniaca* occurs in the foothills of mountains, being highly specialized for deep burrowing (Arakelyan et al. 2018).

Along the Krasnodar coast in Russia, *T. g. ibera* appears in the margins of deciduous forests and open xerophytic shrubland (or *shiblyak*) with a 30–40% cover formed by junipers, Atlantic pistacias (*Pistacia atlantica* var. *mutica*), Christ's thorns and dog roses (*Rosa canina*) with dense grasses (Inozemtsev and Pereshkolnik 1994; Gallyamov 1997; Leontyeva et al. 2001; Leontyeva 2004). A lower terrain slope of <10º favors the local abundance of this species (it rarely occupies habitats with a slope of ≥25°), as does a greater density of grass and less cover of trees and shrubs (Gallyamov 1997; Kuzmin 2002). The highest abundance (>1 individual per km) occurs in *Juniperus-Pistacia* shrubland, with low tree cover and shrubs and dense grass, on flat terraces with southern exposure below 100 m. The lowest abundance (<0.5 individual per km) occurs in oak, oak-hornbeam and hornbeam-alder forests, on hills with ≥10° slope above 200 m (more than 2 km from the coast). Deciduous forests are usually inhabited by older individuals (Gallyamov 1997; Kuzmin 2002).

In Dagestan in Russia, *T. g. armeniaca* occurs on the Sarykum inland dune, on the coastal dunes of the Caspian Sea (mobile sands vegetated with pears [*Pyrus*]*,* buckthorns [*Rhamnus*]*,* and raspberry bushes [*Rubus*]), in sandy semi-deserts (sagebrush-grass semi-deserts, sagebrush-forb semi-deserts, sagebrush-forb-cereal semi-deserts), lowlands vegetated with rushes (*Juncus*) and floodplain forest, on the edge of the delta forest of the Samur River, in dry steppes (grass-wormwood steppes, forb-grass steppes with species of sub-shrubs and grasses: *Teucrium, Eryngium, Salvia, Inula, Dianthus, Festuca, Artemisia, Andropogon, Stipa*), in foothill *shiblyaks* (with species of cherries [*Cerasus*], Jerusalem thorns [*Paliurus*]*,* and salt cedars [*Tamarix*]), in arid and juniper woodlands (with species of *Pyrus*, hawthorns [*Crataegus*]*,* and silverberries [*Elaeagnus*]) and in agricultural landscapes (Mazanaeva 2001, 2009, 2013, 2021; Mazanaeva and Gichikhanova 2018, 2019, 2020b, 2021).

In Georgia, the species occurs in semi-deserts, steppes, and mixed habitats of grassland and shrubs with interspersed patches of forest (Muskhelishvili 1970; Auer and Herz 2021) as well as in highly anthropogenically impacted habitats, including agricultural lands and the surroundings of cities, such as Tbilisi (Kuzmin 2002; Auer and Herz 2021).

In western Armenia, in the Araxes River valley, *T. g. armeniaca* occurs in steppes, with low vegetation and abundant rocks, where it takes refuge in 1 m deep burrows (Zugmayer 1906; Arakelyan et al. 2011, 2018). In southern Armenia, it also occupies steppes (dominated by wormwoods: *Artemisia fragrans* and *A. araxina*), juniper woodland, agricultural lands (e.g., vineyards), and fluvial gorges (Arakelyan and Parham 2008). In northeastern Armenia, *T. g. ibera* occurs at the edges of oak-hornbeam forests (Arakelyan and Parham 2008).

In Azerbaijan, *T. g. armeniaca* occurs in steppes and semi-deserts, in hilly habitats with herbaceous cover and some shrubs, avoiding areas with salinized soils and steep slopes (Alekperov 1978).

In northwestern Iran (Ardabil province), *T. g. buxtoni* inhabits alpine steppes and cultivated land in the lowlands (Rezazadeh et al. 2014). In the center of Iran (Isfahan) it occupies open, dry and rocky environments (Pritchard 1966). *Testudo g. zarudnyi* occurs on steppes, open hills, alluvial plains, and cultivated lands. It is common on plains interspersed with small hills, with a substrate of gravel and rocks and scattered bushes (Javanbakht, unpubl. data). In northeastern Iraq, near the Iran border, *T. graeca* occurs in sparse vegetated habitats, including alpine grasslands in Erbil Liwa (Reed and Marx 1959).

In Jordan, *T. g. terrestris* occupies mixed forests of Aleppo pines (*Pinus halepensis*) and Palestinian oaks

(*Quercus calliprinos*) with an undergrowth of Greek strawberry trees (*Arbutus andrachne*), olive trees (*Olea europaea*) and turpentine trees (*Pistacia terebinthus* var. *palaestina*). Forested habitats are preferred to open habitats and agricultural land; in these forests, tortoises tend to occupy more open patches but with abundant leaf litter where they can take refuge (Attum et al. 2011).

In Israel, *T. g. terrestris* is found in regions with varied vegetation structure, from dense Mediterranean shrubland to grasslands, but is also common in coastal dunes and pine-forested plantations (Buskirk 1967; Maza 2008; Bernheim et al. 2019; Bar et al. 2021; Meiri, unpubl. data). In the northern Negev this tortoise inhabits loess plains, with small dunes and scattered grass tussocks (*Panicum turgidum*; Bringsøe and Buskirk 1998). In Wadi Gaza, it occupies agricultural lands (olive plantations and vineyards) and salt cedar riparian galleries (Rabou et al. 2007).

Daily Activity. — This species is almost exclusively diurnal throughout the region (Wright et al. 1988; Leontyeva 2004; Chkhikvadze 2009; Werner 2016; Bar et al. 2021). In mainland northeastern Greece, activity occurs in summer, with a bimodal activity pattern, between 0800–1100 and 1800–2000 hrs (Wright et al. 1988). On Samothraki Island, Clark (1991) observed *T. g. ibera* foraging early in the morning at 0800 hrs and 23°C. In northern Greece, the average body temperature during activity was 30–31°C, with maximum values of 37°C (Wright et al. 1988). The mean values of body temperature were similar in males (30.3ºC ± 2.0; n = 116) and females (30.8ºC ± 3.1; n = 143; Hailey et al. 1988). In Bulgaria in the spring, tortoises are active typically at 1000–1800 hrs, but their activity becomes bimodal with the warming of the weather; in exceptional cases during extremely hot weather *T. g. ibera* were active at 0130 hrs (Petrov et al. 2004).

Testudo g. ibera in European Turkey is active from early April to late September and, depending on the season, individuals may be observed throughout the day. However, during hot weather in July and August, bimodal activity occurs. The mean body temperature was 27.8°C when they were active in July–August (Türkozan, unpubl. data). In an experiment conducted with Anatolian individuals of *T. graeca*, it was observed that these tortoises regulate their temperature through respiration; they increase their breathing rate progressively when body temperature exceeds 30ºC and exhibit panting above 35ºC. If the body temperature continues increasing (to ca. 39ºC), salivatory thermoregulation starts (Cloudsley-Thompson 1974). The critical thermal maximum is reached around 42.8–43.6°C (Hutchison et al. 1966). *Testudo g. terrestris* from Anamurium (southern Turkey) reduces its activity and hides among bushes in the middle hours of the day during the summer period (Taskavak and Türkozan 2004a).

In Krasnodar (Russia), during the peak activity season in May–June, tortoises are active from 1000 hrs, with body temperatures of 27–30°C (Leontyeva 2004). Activity ceased around 1400 hrs, but some individuals resumed activity between 1700–1800 hrs (Leontyeva 2004). During periods of inactivity, these tortoises bury themselves at the base of thorny bushes. In densely vegetated areas of Dagestan, *T. g. armeniaca* exhibits activity during most of the day, although more active during the morning at an average air temperature of 29.1°C (Bannikov 1951). In steppes, tortoises reduce their daily activity to seven hours or less (Bannikov 1951).

In Armenia, *T. g. armeniaca* is active in the middle of the day during spring, and in summer its activity becomes bimodal, being active in the morning and in the afternoon until dusk. During the inactivity periods it hides at the bases of bushes or in mammal burrows (Taskavak et al. 2004). In northern Israel, activity body temperatures varied between 26.2–36.7°C (Werner 2016).

Annual Activity. — This species shows a winter rest period (much more pronounced in northern populations), which usually extends between late autumn and late winter, and a shorter resting period during mid-summer, particularly in the southern part of the range (Israel, Jordan, southern Turkey). The period of maximum activity extends between the end of winter and the beginning of summer, with a small rebound at the end of summer.

In northeastern Greece and Bulgaria, *T. g. ibera* is active between March and October–November (Wright et al. 1988; Petrov et al. 2004; Ivanchev 2007; Stojanov et al. 2011). In southern Turkey (Anamurium), *T. g. terrestris* leaves hibernation shelters on sunny days at the end of January–February (Taskavak and Türkozan 2004a); in Samandagi, tortoises also leave hibernation shelters at the end of January–February, but more frequently in March, and remain active until the end of October (Taskavak and Türkozan 2004b). An estivating male *T. g. terrestris* was found in Yayladağ, southeastern Turkey during midday in July (Ayaz and Çiçek 2011).

In Krasnodar (Russia), *T. g. ibera* hibernates between October and the end of April or May (Leontyeva 2004). Peak activity occurs in May and June (Leontyeva 2004). In summer (between the end of July and August) tortoises reduce their activity and migrate into valleys where they find more food (Leontyeva 2004). In Dagestan in Russia, daily activity varies depending on the biotope and season. Single-peak activity is typical during spring and autumn. Tortoises are active from 0900 to 1700 hrs, with a peak of activity between 1100 to 1600 hrs. The optimal temperature range for activity is 21–25°C. In summer, activity shifts to morning (0800–1200) and evening (1800–2100) hours. In open landscapes, at temperatures above 28–30°C, activity ceases completely, but in forested biotopes, activity can persist. In the second half of summer, when the air temperature rises above 30°C, tortoises often estivate until temperatures drop again (Bannikov 1951; Mazanaeva 2013). According to Bannikov (1951) tortoises end hibernation in Dagestan in the first half of March, and return quite early, usually during mid- or early October. Tortoises overwinter in the same shelters used during the spring and summer. In the foothills of Dagestan, the species is active from late April to late October–early November and on the Caspian coast it is active from early March to late October, depending on weather conditions (Gichikhanova et al. 2019).

In Armenia, *T. g. armeniaca* is active between mid-March and mid-October, although it exhibits less activity in the warmer periods of summer (Arakelyan et al. 2011). In Iran, *T. g. buxtoni* is active between mid-April and late October (Javanbakht, unpubl. data).

In the mountains of Jordan, *T. g. terrestris* hibernates between November and February, showing a peak of activity during March and April. Estivation occurs during August and September, with a second peak of activity in October (Attum et al. 2011). In lowland areas of northern Israel, *T. g. terrestris* does not hibernate, and is usually active on sunny winter days (Meiri and Shanas, unpubl. data), but is more active between March–May and October–November, with a marked activity hiatus for estivation during the hot summer months (Bernheim et al. 2019).

Home Range. — In the mountains of Jordan, home activity ranges were less than 10 ha (Attum et al. 2011). In northern Israel, the mean home range was 1.489 ± 0.29 ha for radio-transmitted individuals, showing a wide overlap within and between sexes and throughout the year, including the breeding season (Bernheim et al. 2019).

Reproduction. — The breeding season begins at the end of hibernation, which occurs between mid-winter (January) and mid-spring (May) depending on local climate conditions. Egg incubation usually lasts between 2–3 months, and hatchlings appear at the end of the summer, although in the extreme north of the distribution range (southwestern Russia) hatchling emergence usually occurs in the following spring (Leontyeva 2004; Jasser-Hager and Winter 2007).

In northern Greece (*T. g. ibera*), mating occurs between March and May, with a second period at the end of the summer, in mid-August and September. During courtship, the male usually walks behind the female, striking the back of the female 2–4 times with the frontal part of the plastron. Three males repeated butts at rates of 11, 30, and 39 minutes; one male made 113 butts in 10 minutes (Hailey 1990). Oviposition begins in May and extends until mid-June. In northern Greece, females lay 4–5 eggs two times per year. Egg size varies between 23 × 33 mm to 48 × 49 mm, with an average weight of 25 g (14–33 g; Jasser-Hager and Winter 2007). Hatching occurs after 54–89 days of incubation (mean 62 days), from the end of August to the beginning of September (Jasser-Hager and Winter 2007).

In Bulgaria, copulation is typically in the spring (March–April), but also in mid- to late summer (July–September) (Petrov et al. 2004). Three to seven eggs are laid 2–3 times in May and July, usually at the base of a south-facing slope (Petrov et al. 2004).

In central Turkey (Nevşehir, Cappadocia), female *T. g. ibera* laid an average of 2.33 eggs per clutch (range 1–8) averaging 31.4 × 35.5 mm in size (mean egg mass 18.3 g; Akveran and Ayas 2019). In southern Turkey (Anamurium), female *T. g. terrestris* reach sexual maturity at 14.3 cm SCL and lay between 15–19 eggs per year between April and May, divided into three clutches (Berglas 2000; Taskavak and Türkozan 2004a). Eggs hatch after 58–83 days at temperatures of 23–36°C and humidity of 35–70%, with a success rate of 55–70% (Taskavak and Türkozan 2004a). Mean SCL of hatchlings was 4.7 cm ± 0.04 SD (range 3.8–5.6 cm) and with a mean body mass of 24 g ± 0.6 SD (range 14–41 g) (Taskavak and Türkozan 2004a). In Samandagi, females reach sexual maturity at 14.2 cm SCL and a single female laid 8 eggs, divided into 2 clutches (Taskavak and Türkozan 2004b). Under the same nest conditions as in Anamurium, 63–71% of the eggs hatched after 64–90 days (Taskavak and Türkozan 2004b). The mean SCL of the hatchlings was 4.0 cm ± 0.04 SD (range 3.1–5.2 cm) and the mean body mass was 23.1 g ± 0.6 SD (range 13–40 g) (Taskavak and Türkozan 2004b).

In Krasnodar, Russia (*T. g. ibera*), mating occurs shortly after hibernation ends. Courtship is aggressive and includes the male ramming and biting the female (Boiko 1984). Oviposition occurs in May, and clutches contain 4–6 eggs (Leontyeva 2004). Females nest in open and sloped terrain within forests. Hatchlings overwinter in the nest chamber and usually remain buried until emerging in the spring of the following year (Leontyeva 2004; Mazanaeva, pers. comm.).

In Dagestan, Russia, *T. g. armeniaca* starts mating immediately after emerging from hibernation, from the second half of April to mid-June, most actively in late April–May. In high-density populations, it mates throughout the entire period of activity. Oviposition occurs in the second half of May and early June, with either 3 clutches of 3–8 eggs per season (Bannikov 1951) or 2 clutches of 6–8 eggs (Mazanaeva 2009, 2013, 2021). The eggs are almost spherical, 32–36 mm in diameter with a mass of 22–23 g, with a white calcareous shell. Eggs are laid in cavities dug at the roots of shrubs or in an open area, mostly in loose soil, and are covered with soil. The nest chamber is jug-shaped with a wide mouth. The bottom of the cavity is somewhat convex, so that the eggs are located along its edges, and are to some extent protected by the harder surrounding undisturbed ground. The female digs the cavity for 15–20 min, but the interval between the laying of each egg can be up to 20–30 min. After the last egg is laid, the female remains motionless for some time, and then with its hindlimbs covers the nest with soil. When the nest is entirely filled, the female packs the loosened ground with her plastron. The incubation period lasts 2–3 months. Hatching occurs in September with a hatchling SCL of 35–45 mm, and hatchlings display a secretive lifestyle until the next spring. Sexual maturity is reached at the age of 12–14 yrs at an SCL of approximately 16–18 cm (Bannikov 1951; Mazanaeva 2009, 2013, 2021; Mazanaeva and Gichikhanova 2020a,b).

In Armenia (Araxes Valley), *T. g. armeniaca* starts mating after hibernation (mid-March) and continues until the end of May or, occasionally, until the second half of June (Arakelyan et al. 2011). Egg-laying occurs at the beginning of June. Females are sexually mature at an SCL of 11.8 cm (Taskavak et al. 2004). Females lay their eggs after digging nest chambers of 12 × 17 cm (Arakelyan et al. 2011). The number of eggs produced by females varies with SCL: 11.8–13.5 cm females produce 1 clutch of 3–5 eggs, 14.1–20.4 cm females produce 2 clutches, totaling 7–13 eggs per year, and 21.6–25.8 cm females produce 3 clutches, totaling 15–19 eggs per year (Taskavak et al. 2004).

Hatchlings have a mean SCL of 3.9 cm ± 0.02 SD (range 3.2–4.1 cm), and mean body mass of 14.9 g ± 0.2 SD (range 9–19 g; n = 79). At one year of age, juveniles have a mean SCL of 6.0 cm ± 0.02 SD (range 5.9–6.6 cm), and mean body mass of 49.4 g ± 0.6 SD (range 42–64 g; n = 56); at two years of age, juveniles have a mean SCL of 8.0 cm ± 0.06 SD (range 7.5–8.8 cm), and mean body mass of 98.1 g ± 2.84 SD (range 69–140 g; n = 34); and at four years of age, juveniles have a mean SCL of 8.1 cm ± 0.09 SD (range 7.6–8.4 cm) and mean body mass of 118.8 ± 4.12 SD g (range 94–135 g; n = 11) (Taskavak et al. 2004).

In central Iran (*T. g. buxtoni*), courtship behavior was observed in the spring (Sadegui and Torki 2012; Javanbakht, unpubl. data), but also in September (Pritchard 1966). Courtship consists of four phases: (1) aggression: the male follows the female, butting her with his carapace from behind with his head retracted, and biting her hind legs, neck, or head while the female tries to escape; this phase can last from 10 to 50 min; (2) submission: the female stops moving in response to the aggressive behavior of the male; (3) copulation: the male mounts the female, with his neck extended and his mouth open, with the carapace at 50° with respect to the horizontal; copulation can occur between 5–21 times per pair and each one lasts between 10–70 sec; the male usually emits high-pitched noises and the female moves her head laterally repeatedly; and (4) resting: after mating, the male and female rest together for a short period of time (Pritchard 1966; Sadegui and Torki 2012).

Females begin egg-laying in May, excavating a nest chamber 13 cm deep and 5 cm wide, spending about 10 min in this process, laying 4 eggs averaging 34.9 × 44.9 mm (31.6–34.9 × 43.4–45.9 mm, mass 26–30 g), 75% of which hatch after 72–75 days, with hatchlings measuring 35.7–40.8 mm SCL (Sadegui and Torki 2012).

In coastal areas of Israel, *T. g. terrestris* mate for about a month, starting in mid-winter (January); however, some mating also occurs in autumn (Perälä and Shacham 2004). Males reach sexual maturity at an SCL of around 10 cm (approximately at an age of 6–7 yrs; Buskirk 1967; Shanas, unpubl. data). Egg-laying occurs primarily in mid-June (April–June or May–July; Lapid and Robinzon 1995; Perälä and Shacham 2004), and usually consists of 1–3 clutches of 1–7 eggs (Lapid and Robinzon 1995). Clutch size is 3.8 eggs on average (in 18% it is divided into two clutches, separated by 11–21 days; Lapid and Robinzon 1995; Werner 2016). The female digs a nesting chamber 10–15 cm deep and deposits 2–4 or 3–5 eggs of 30 × 40 mm (Perälä and Shacham 2004; Werner 2016). Incubation lasts about 3 months (or 103 ± 3.1 days, under natural conditions) with hatching occurring in September, with hatchling SCL averaging 35 mm (Arbel 1984; Lapid and Robinzon 1995; Werner 2016). The natural hatching rate was 28% (Lapid and Robinzon 1995).

Testudo g. terrestris has temperature-dependent sex determination, with a pivotal temperature of 30.5 ± 0.5ºC (Bernheim 2014).

Demographics. — In most populations not negatively impacted by humans, there is evidence of a trend towards a greater relative proportion of males. The low proportion of recorded juveniles is likely due to their low detectability and possibly does not reflect the true demographics (Leontyeva et al. 2001).

In three coastal localities in northern Greece (Epanomi, Keramoti and Lagos), the density of *T. g. ibera* ranged between 7–21 individuals per ha (Hailey et al. 1988). The individuals found ranged between 11–53% males, 17–45% females and 3–73% juveniles (Hailey et al. 1988). On Thasos Island (northern Greece), 53% of sampled *T. g. ibera* were males, 32% females, and 12% juveniles (3% undetermined; n = 68) (Cattaneo 2001).

In Bulgaria (Eastern Rhodopes), the sex ratio was skewed towards males, both in areas before being burned (1.4:1; n = 49; males = 19, females = 14, juveniles = 16), and in control areas (1.32:1; n = 77; males = 37, females = 28, juveniles = 12). In areas that burned, surviving males were again more numerous after the fire (2.1:1; n = 40; males = 17, females = 8, juveniles = 15), while females were more numerous among the deceased individuals (3:1; n = 9; males = 2, females = 6, juveniles = 2). The ratio of adult: juvenile *T. g. ibera* before the fire was 2.75:1, and after the fire this ratio was 1.7:1 for the live captures, and 4:1 for the dead individuals (Popgeorgiev 2008).

In the Gediz Delta of western Turkey, of a total of 114 individuals of *T. g. ibera*, 54% were males, 28% were females, and 18% were juveniles (Arslan et al. 2021). In

European Turkey, of 197 individuals, 57% were males, 28% were females, and 15% were juveniles (Türkozan, unpubl. data).

In the Abrau Peninsula (Krasnodar, Russia), adult individuals (i.e., SCL ≥ 17.5 cm, corresponding to ca. 25–30 yrs old) predominate, constituting 72.8% of males and 65.9% of females (Leontyeva et al. 2001). In a sample of 96 individuals, the proportion of adult males and females was identical (43%), with a low proportion of juveniles (SCL < 15 cm; 14%) (Leontyeva et al. 2001). In the Cape Utrishonok population (Mys Malyy Utrish; Abrau Peninsula), 22% of the individuals had carapace lengths between 3.5–13.5 cm (juveniles), 8% between 13.5–18.5 cm (subadults), and 70% between 16.0–21.0 cm (males) and 18.5–24.0 (females) (Galichenko 1997).

In Dagestan, in the coastal lowlands of the Caspian Sea (Primorskaya lowland), in a sample of 75 individuals, 59% were females, 32% males, and 9% juveniles; however, the proportion of juveniles can be adversely biased due their secretive lifestyles (U.A. Gichikhanova, pers. comm.).

Longevity. — Slavens and Slavens (1990) reported a lifespan of 127 years in captivity for a *T. graeca* of unknown origin, and Murphy (2016) recorded maximum lifespans of 128 and 148 years in captivity for individual *T. graeca* western subspecies clade animals. Galichenko (1997) reported maximum longevity of over 55 years for eastern subspecies clade animals (*T. g. ibera*) in the wild.

Diet. — These tortoises are generalist herbivores and in nature they feed on dry plant matter, leaves and flowers of seasonal plants, specifically including the families Amaryllidaceae (amaryllids), Asteraceae (daisies), Fabaceae (legumes), Lamiaceae (mints), Plumbaginaceae (plumbagos), and Poaceae (grasses) (e.g., genera *Acantholimon*, *Andropogon*, *Allium*, and *Salvia*), and their seeds, fruits of cultivated plants (carob tree, pomegranates, figs, grapes, and apricots) and occasionally animal matter such as worms, snails (*Helicella*), arthropods (beetle larvae), and carrion (Bannikov et al. 1977; Arakelyan et al. 2011; Werner 2016; Bar et al. 2021).

In northeast Romania, the diet of approximately 500 wild individuals of *T. g. ibera*, sampled over 10 years (Iftime and Iftime 2012), was 96.5% herbivorous, based on leaves and flowers of 25 plant species of the families Amaranthaceae (*Atriplex*, *Amaranthus*) (pigweeds), Asteraceae (*Taraxacum*), Fabaceae (*Lotus, Medicago, Trifolium*), Lamiaceae (*Teucrium*), Poaceae (*Dactylis, Dichantium, Festuca, Poa*), Polygonaceae (*Polygonum*) (knotweeds), Ranunculaceae (*Ranunculus*) (buttercups), Rosaceae (*Fragaria, Rosa*) (roses), Rubiaceae (*Galium*) (madders), and Vitaceae (*Vitis*) (grapevines) and occasionally the fruits of small trees such as *Cornus mas*, and species of the genera *Pyrus* (pear trees) and *Prunus* (apricot trees). The most frequently consumed vegetable materials were young leaves of *Ficaria, Taraxacum, Lotus, Trifolium, Medicago, Fragaria, Polygonum,* Poaceae*, Sonchus*, and *Teucrium* and more rarely those of Apiaceae (celeries), Asteraceae (*Artemisia*), Chenopodiaceae (goosefoots), Lamiaceae, Rosaceae (*Rosa*), and Rubiaceae (Iftime and Iftime 2012). Tortoises also consumed some animal matter, but with low frequency: carrion from a wild cat, birds, bovines and sheep, and leftovers from the prey of jackals and dogs. In addition, juveniles and subadults sometimes consume friable limestone rock as a source of calcium.

In Dagestan, the range of *T. g. armeniaca* diet in the foothills is broader than in the Caspian Sea coastal lowlands (U.A. Gichikhanova, unpubl. data). In the foothills, diet included plants from 16 families (Asteraceae, Fabaceae, Primulaceae, Liliaceae, Malvaceae, Asparagaceae, Poaceae, Rosaceae, Plantaginaceae, Lamiaceae, Hyacinthaceae, Polygonaceae, Iridaceae, Convolvulaceae, Boraginaceae, Vitaceae). In the coastal lowland of the Caspian Sea, diet included plants from nine families (Asteraceae, Fabaceae, Papaveraceae, Poaceae, Plantaginaceae, Malvaceae, Rosaceae, Hyacinthaceae, Convolvulaceae). Two peaks of feeding activity were observed: in spring (April–May) and in autumn (September–October). First, tortoises eat flower heads, then succulent leaves and stems. In the spring, during the growing season, tortoises mainly feed on ephemera and ephemeroid plant groups (Papaveraceae, Liliaceae, Asparagaceae, Primulaceae), and after the flowering period they feed on plants from other families. In the summer, when the vegetation dries up, they switch to Poaceae (cereals) or stop feeding. In the autumn, when ephemera and ephemeroids revegetate, tortoises feed on succulent herbaceous vegetation (Plantaginaceae, Lamiaceae, Hyacinthaceae, Polygonaceae, Iridaceae, Convolvulaceae, Beraginaceae, Vitaceae, Rosaceae). In the absence of plant matter, the tortoises can also eat insect larvae (U.A. Gichikhanova, unpubl. data).

Predation. — In the eastern Mediterranean Basin and southwestern Asia, large eagles and canids and other generalist predatory mammals opportunistically prey on adults of *T. graeca* (Chkhikvadze 2009; Demerdzhiev et al. 2014, 2022). On the other hand, juvenile individuals are frequently depredated by large colubrids and large lizards, owls, crows, magpies, raptors, mustelids, and wild canids (Stanner and Mendelssohn 1987; Chkhikvadze 2009; Sadegui and Torki 2012; Mazanaeva 2013).

In Greece and Bulgaria, adult *Testudo* spp. are depredated by Golden Eagles (*Aquila chrysaetos*), Eastern Imperial Eagles (*Aquila heliaca*), and Egyptian Vultures (*Neophron percnopterus*) (Simeonov et al. 1991; Undzhiyan 2000; Iankov 2007; Dobrev et al. 2015; Demerdzhiev et al. 2022; Milchev 2022). Until the 1990s, tortoises numerically comprised up to 50% of the diet of Golden Eagles in the Strandzha Mountains of southeastern Bulgaria, but

Figure 15. Golden Eagle (*Aquila chrysaetos*) in Israel after capturing an adult *T. graeca terrestris*. Photo: Liron Shapira.

this amount dropped to 5.8% between 2014–2021 due to a collapse of tortoise populations (Milchev 2022). Individual birds or pairs may feed exclusively on tortoises; however, these predators' populations are relatively low in number and likely do not pose a threat overall. Rarely, eggs and young tortoises are consumed by Beech Martens (*Martes foina*), European Badgers (*Meles meles*), Red Foxes (*Vulpes vulpes*), Golden Jackals (*Canis aureus*), feral dogs (*Canis familiaris*), and Common Ravens (*Corvus corax*); adults may become prey of Wild Boars (*Sus scrofa*) (Beshkov 1984; Petrov et al. 2004). *Testudo* spp. were also consumed by White Storks (*Ciconia ciconia*) and Short-toed Eagles (*Circaetus gallicus*) and *T. g. ibera* remains were found in the nest of a Eurasian Eagle Owl (*Bubo bubo*) (Tzankov and Milchev 2014).

In European Turkey, *T. g. ibera* and *T. hermanni* accounted for a total for 14.4% of the prey caught by sampled Eastern Imperial Eagles (Demerdzhiev et al. 2014). In Dagestan, eggs are devoured by mammals: Red Foxes, feral dogs, Golden Jackals, Raccoon Dogs (*Nyctereutes procyonoides*), and White-breasted Hedgehogs (*Erinaceus concolor*) and birds (sea gulls and crows). Juveniles are depredated by mammals (foxes, Eurasian Wolves [*Canis lupus*], jackals, dogs), birds (sea gulls, raptors, crows), and some large snakes and lizards: Caspian Whip Snakes (*Dolichophis caspius*), Red-bellied Whip Snakes (*Dolichophis schmidti*), and Pallas' Glass-lizards (*Pseudopus apodus*) (Mazanaeva 2001; Mazanaeva et al. 2009). Larger birds of prey pick up these tortoises and drop them on rocks during predation attempts, and individuals with damaged carapaces are often encountered. In agricultural lands, tortoises with damaged carapaces from cattle hooves are also detected (Mazanaeva 2013). In Georgia, the eggs of *T. g. ibera* are eaten by rodents and birds (Eurasian Magpies, *Pica pica,* and Hooded Crows, *Corvus cornix*) and juveniles by large snakes (Chkhikvadze 2009). Adults can be attacked by Striped Hyenas (*Hyaena hyaena*) (Vekua et al. 1980).

In central Iran (Zagros Mountains) tortoise hatchlings are depredated by birds (crows and ravens) and carnivorous mammals, and adults by eagles, feral dogs and wolves (Sadegui and Torki 2012). In northeastern Iraq, Reed and Marx (1959) reported an adult tortoise with deep injuries on the carapace, which they attributed to an attack by a Brown Bear (*Ursus arctos*).

Buskirk (1967) noted that tortoises in the Haifa Plain of northern Israel are preyed upon by Egyptian Vultures, Golden Jackals, and Striped Hyenas, and that individuals from the mountains more frequently had damaged carapaces than those found in the lowlands. Juvenile tortoises in Israel are depredated by Hooded Crows and Egyptian Vultures and Little Owls (*Athene noctua*) (Mienis 1979; Perry and Dmi'el 1995). There are also records of Golden Eagles that drop tortoises from the air onto rocks to break the shell and access the fleshy parts. In the southern coastal plains of Israel and in the Negev, carapace remains of juvenile tortoises have been found depredated by crows (up to 40 tortoise shells under a single tree) and in the droppings of the Desert Monitor (*Varanus griseus)* (Stanner and Mendelssohn 1987; Mendelssohn and Geffen 1995; Mendelssohn *in* Bringsøe and Buskirk 1998).

Cheloniophagy by humans may have had some relevance in Ancient Chalcolithic communities from southeastern Europe, where carapace remains of tortoises (*T. g. ibera*) and freshwater turtles (*Emys orbicularis*) have been found in archaeological sites dated from this period (4000 BP, Durankulak, northeastern Bulgaria; Schleich and Böhme 1994). In Iran, Ashayer nomadic herders in the Zagros Mountains use tortoises opportunistically as a food source (Sadegui and Torki 2012). In the 18th century, tortoises were sold in public markets as food in Syria and Lebanon and Eastern Christians drank the blood of tortoises during the fasting season or Lent (Niebuhr 1792). In Israel, tortoises were exploited for food by humans since the Middle Pleistocene (e.g., Maul et al. 2016; Smith et al. 2016) – and especially since the Natufian period ca. 12,000 years ago (Stiner et al. 1999) and until the agricultural revolution (e.g., Khalaily et al. 2007). In the present they are sometimes illegally caught for food by itinerant workers (Yom-Tov 2003).

Testudo graeca may survive some major injuries, impacting up to 50% of the carapace—in Romania, surviving individuals of *T. g. ibera* have been found that appear healthy despite suffering severe mechanical trauma by agricultural machinery, which caused the destruction of most of the vertebral scutes and parts of the costal scutes (Sos 2012).

Parasites and Ectobionts. — Fungal infections have been described in *T. g. ibera* in Gelendzhik, Krasnodar, Russia, affecting 85% of the adult individuals from the same locality (Kuzmin 2002). *Testudo g. ibera* can be the host for several species of endoparasitic protozoa: *Entamoeba testudinis*, *Haemoproteus caucasica*, *H. ibera*, *Monocercomonas testudinis*, *Opalina zasukhini*, *Plasmodium* *smirnovi,* and *Proteromonas ophisauri* (Muskhelishvili 1970; Kuzmin 2002).

In Turkey, *T. g. ibera* is also infected by the protozoan *H. anatolicum* (Orkun and Güven 2013). In Bulgaria, 14% of wild individuals of *T. g. ibera* were infected by apicomplexan parasites (*Hemolivia mauritanica*), while in Greece it was 81% and in Turkey 92% (Široký et al. 2005). In Romania, *H. mauritanica* has also been detected in wild *T. g. ibera* (Mihalca et al. 2008). In Iran, 52.5% of tested *T. g. buxtoni* were infected by *H. mauritanica,* but the prevalence varied geographically, being higher in western mesic regions, but there were no differences between males and females or among age groups in the intensity of parasitemia (Javanbakht et al. 2015).

Numerous species of helminths of the families Anisakidae and Oxyuridae have been described in the eastern subspecies of *T. graeca*: *Alaeuris numidica, Mehdiella microstoma, M. stylosa, M. uncinata, Tachygonetria conica, T. dentata, T. longicollis, T. microlaimus, T. numidica, T. palearcticus, T. pusilla, T. robusta, Thaparia thapari,* and *Angusticaecum holopterum* (Bouamer and Morand 2006). In western Turkey (Bursa) seven species of helminths have been detected in the intestinal tract of *T. g. ibera*: *Atractis dactyluris, A. holopterum, M. microstoma, M. uncinata, T. conica, T. dentata,* and *T. longicollis* (Yildirimhan et al. 2018; Ceylan et al. 2020). In Iraq (Mawat, Rabia'a), *A. holopterum* and *A. dactyluris* were found (Al-Barwari and Saeed 2007).

On the Greek island of Samothraki, *T. g. ibera* has been noted to be infested by the tick *Hyalomma aegyptium*, which can be found on the forelimbs, hindlimbs, and neck (Clark 1991). This tick species also infested mainland populations of *T. g. ibera*, and both sexes had similar levels of tick infestation, with the mean number of ticks per adult tortoise ranging between 2.06–3.80 in males and 2.17–3.29 in females (Hailey et al. 1988). The number of ticks per individual was higher in *T. g. ibera* than in sympatric *T. hermanni boettgeri* (Hailey et al. 1988).

Hyalomma aegyptium is the only adult stage tick found on Balkan populations of *T. g. ibera*; however, larval and nymphal forms of *Haemaphysalis sulcata* can also be found, notably when *T. g. ibera* occurs in sympatry with *T. hermanni*, the usual host of adult stages (Široký et al. 2006). *Hyalomma aegyptium* also infests *T. g. ibera* in eastern Romania (Široký et al. 2006; Paştiu et al. 2012), and in this region ticks are essential vectors and zoonotic pathogens (*Anaplasma phagocytophilum*, *Ehrlichia canis,* and *Coxiella burneti*), although tortoises are not their reservoirs and these pathogens may have been acquired following infestation in early developmental stages of competent mammalian reservoirs (Paştiu et al. 2012).

In the Abrau Peninsula (Krasnodar, Russia), *H. aegyptium* only appeared on tortoises and not on other sympatric species such as hedgehogs, dogs, or domestic cats (Leontyeva et al. 2016); however, the adult form of this species occasionally parasitizes hedgehogs and hares, at least in Turkey (Hoogstral and Kaiser 1960). All ticks infesting *T. g. ibera* in Krasnodar were *H. aegyptium* (Robbins et al. 1998). Adult animals were more infested than juveniles and males were more infested than females, presumably because adult males were more active (Robbins et al. 1998; Leontyeva et al. 2016). The mean number of ticks in males was 6.7 ± 0.7 SD, while in females it was 2.4 ± 0.5 SD (Robbins et al. 1998). The number of ticks was significantly reduced in individuals with SCL ≤ 15 cm and they do not appear in individuals with SCL ≤ 8 cm (Leontyeva et al. 2016). According to Leontyeva et al. (2016) there could be infestation peaks every 11 years.

In Dagestan, tortoises are usually parasitized by *H. aegyptium*, appearing in the folds of the skin of the fore- and hind limbs, as well as the neck. Rarely the ticks were found on the carapace, where they attach between the horny scutes. In addition, tortoises can host endoparasites (Nematoda; U.A. Gichikhanova, pers. comm.). *Hyalomma aegyptium* also parasitizes *T. g. armeniaca* in Azerbaijan and *T. g. terrestris* in Lebanon, up to a maximum of 100 ticks per tortoise (Reed and Marx 1959; Alekperov 1978; Kuzmin 2002).

In northwestern Iran (West Azerbaijan Province) all ticks found on *T. g. buxtoni* were *H. aegyptium* (Tavassoli et al. 2007). In a sample of 32 *T. graeca,* 44% were parasitized by 1 to 60 ticks, mainly attached in the axillary and inguinal regions (Tavassoli et al. 2007). *Hyalomma aegyptium* infests *T. g. zarudnyi*, in Kerman, southern Iran (Nabian and Mirsalimi 2002) and *T. graeca* in Iraq (Reed and Marx 1959; Kheirabadi et al. 2016).

Testudo g. terrestris from the lowlands of Haifa, northwestern Israel, are not usually parasitized by ticks, while those of the mountainous areas are very frequently infested (Buskirk 1967). Similarly, Paperna (2006) reported that the populations in the Golan Heights and Kanaf were infested by *H. aegyptium*. These ticks were vectors of Adeleorina apicomplexan parasites (*H. mauritanica*), although only in the northern Golan Heights (Paperna 2006). A sample of wild *T. g. terrestris*, captured in the surroundings of Jerusalem, Gush Alonim, and Mt. Hermon, harbored *H. aegyptium*, and *Rickettsia africae, R. aeschlimannii*, *Coxiella burnetii, Hemolivia mauritanica, Babesia microti, Theileria* sp., and *Leishmania infantum* were also detected (Mumcuoglu et al. 2022).

Population Status. — *Testudo graeca* shows important local variations in its population density, which depends on the thermal quality of its habitats (lower density in more densely forested habitats) and the degree of agricultural development (drastically decreasing the abundance of this species when it starts to be mechanized; Kuzmin 2002).

In southeastern Bulgaria (Eastern Rhodopes), a region with high abundance of tortoises (Beshkov 1984), the density has been estimated at 2 individuals/ha (95% CI = 1.4–3.0; n = 96) in non-burned areas (Popgeorgiev 2008).

At the edges of Sazlıgöl marshes in the northeastern Gediz Delta of western Turkey, in a study area with an estimated population size of 137 ± 27 individuals, the density was 5.7 individuals per ha. The age structure (using scute rings) indicated that the 11–15 yr age group was the most frequent (37.5%) in the population. Furthermore, 26% of the individuals showed carapace injuries and 3% were dead (Arslan et al. 2021). In European Turkey, 31% of the individuals belong to the 11–15 yr age group, followed by 6–10 (18.1%) and 16–20 (12.4%) yr age groups. Of 210 individuals, 79.5% were healthy (no injuries on the shell), while the rest were either injured (fractures on the carapace) or dead (Türkozan, unpubl. data).

On the Abrau Peninsula of Krasnodar, Russia, the density was estimated at 0.5–1.0 individuals/km^2 (0.005–0.01 individuals/ha); this population remained stable during 9 years of surveys (1991–2000) (Leontyeva et al. 2001). In other regions of Krasnodar, in Anapa-Novorossiyskla, the density was estimated at 5–8 individuals/km^2 (0.05–0.08 individuals/ha), with a total population around 25,000–30,000 individuals in the early 1980s. However, in 1991 the density decreased to 3–5 individuals/km^2 (0.03–0.05 individuals/ha), with a total population around 10,000 individuals (Plotnikov 1991). In 1991, in Sochi National Park (Russia), the population density was estimated at 0.2 individuals/ha (Mazanaeva et al. 2009).

There are currently five populations of *T. g. armeniaca* in Dagestan: three in the foothills (in the northeast, central, and southeast) and two on the coastal lowland of the Caspian Sea (Primorskaya lowland). The extent of protected areas within the species' range is estimated at 106,600 ha. Since the beginning of the 21st century, the area of the species' range in the republic has decreased by more than 70%. Along the coastal lowland of the Caspian Sea, viable tortoise populations persist in the vicinity of Lake Papas (Adzhi), with a suitable habitat area of 1300 ha and in the Samur Delta (2100 ha). In the foothills, viable populations are found in three areas: in the southeastern foothills, from the left bank of the Samur River to the northeastern slopes of the Sabnov-Dzhalgan Range (28,340 ha); the surroundings of the village of Shalasi to the Gamriozen River (6650 ha); and the slopes of the Kanaburu and Narat-Tyube ridges (36,920 ha) (Mazanaeva 2001, 2009, 2013, 2021; Mazanaeva and Gichikhanova 2018, 2019, 2020b, 2021). High population densities have been detected in the floodplain of Rubas (2.3 individuals/ha), and the dune systems around Ozero Palas and Berikei (0.75–1.5 indviduals/ha). In Gurbuki (Shakhre mountain), the population density was 0.5 individuals/ha (Mazanaeva et al. 2009). In the open forests of oaks with junipers at the foot of the mountains, such as near Kukurtbash, *T. g. armeniaca* reached densities of 1.2 individuals/ha (Mazanaeva 2001). Further south, near the border with Azerbaijan, this species occupies shrubby formations at the foot of the mountains, where the population was estimated at 0.5 individuals/ha (e.g., in Dzhalgan mountains; Mazanaeva 2001).

Threats to Survival. — Eastern *T. graeca* is still common throughout its wide range, although some populations are locally threatened. Some parts of Armenia, Azerbaijan, Bulgaria, Romania, and southwestern Russia have seen drastic decreases in this species since the middle of the 20th century (Beshkov 1984; Kuzmin 2002; Mazanaeva et al. 2009; Arakelyan et al. 2011; Moraru et al. 2016). The major threats that currently affect this species are the rapid loss of habitat and habitat quality, including urbanization and land development, mechanized agriculture, bush fires, and population fragmentation.

The previously high impact of the illegal trade has decreased somewhat in recent years, thanks to increased international regulation of trade in protected species (Ljubisavljević et al. 2011; Sadegui and Torki 2012; Werner 2016; Arsovski and Sterijovski 2019). Between 1975–2005, a total of 2,062,289 individuals of the genus *Testudo* were recorded as being traded globally (of which 67% were wild individuals), with *T. graeca* accounting for 37% of the exports (Türkozan et al. 2008).

Tortoise trade has been an important economic activity in the current republics of the former Yugoslavia, with an estimate of 2615 tons of tortoises having been exported over 41 years (mid- to late 20th century), reaching a peak of 80 tons/year during the 1960s; this figure corresponds to approximately 2 million tortoises (Ljubisavljević et al. 2011). Of these, the largest portion corresponded to *T. hermanni boettgeri*, but *T. g. ibera* represented about 34% of the total (Ljubisavljević et al. 2011). The primary importer of the tortoises was Germany. Fortunately, harvesting is currently much more regulated by national and international nature protection laws, including inclusion in CITES Appendix II since 1975 (Ljubisavljević et al. 2011).

In northeastern Greece, *T. g. ibera* is mainly threatened by mechanized agriculture and periodic agricultural fires (Willemsen and Hailey 1989). In Bulgaria, fires cause mortality of juveniles and adults, and particularly impacts females, reducing densities over 4.2 times in the Eastern Rhodopes (Popgeorgiev 2008). In eastern Bulgaria, this species was common until the end of the 20th century (Beshkov 1984); many populations have declined in recent years due to multiple, mostly anthropogenic factors, including poaching for pet trade and consumption, involving at times over 200–600 individuals/year (*T. g. ibera* and *T. hermanni*), and habitat loss (Takacs 1987; Petrov et al. 2004; Petrov 2007; Popgeorgiev 2008; Beshkov 2015).

In Turkey, populations of *T. graeca* are threatened by habitat loss and degradation, ongoing illegal trade from the wild, and the use of pesticides. Additional threats are livestock overgrazing, uncontrolled burning for agricultural activities, and urbanization (Arslan et al. 2021). Tortoises are largely appreciated by the locals, e.g., individuals found in crop fields are often transported to other places with natural vegetation (Türkozan, pers. comm.). However, the intensive use of heavy machinery during the harvest causes serious injuries or death of many *T. graeca* in crop fields. Forest fires, causing the death or serious injuries of hundreds of tortoises, are particularly frequent along the Aegean and Mediterranean regions of Turkey (Türkozan, pers. comm.).

Turkey accounted for 19% of the global *Testudo* trade between 1974–2004, and *T. graeca* accounted for ca. 80% of this trade. The main importer at that time was the United Kingdom (63% of the trade) (Türkozan and Kiremit 2007). According to Klemens (2000), Turkey was the main supplier of *Testudo* between 1980–1985, exporting at least 263,000 individuals to Europe. After the import restriction by the European Union in the late 1980s and Turkey being a party to CITES regulations since 1996, *Testudo* trade from the wild was drastically reduced (Türkozan and Kiremit 2007).

In southern Russia, a significant decline of *T. g. armeniaca* has been observed recently, linked to habitat loss (deforestation, cattle overgrazing, and land fencing), agricultural fires, the use of pesticides, direct destruction by humans and domestic animals, road mortality, as well as illegal collection for sale (Mazanaeva 2001; Mazanaeva and Gichikhanova 2018, 2019). Some populations located near cities such as Izberbash, Derbent, Dagestankie Ogni, Belidzhi, and Khazar have almost completely disappeared (Mazanaeva 2001). In the city of Makhachkala the species was present on the Tarki-Tau Mountain until the 1980s, but this population has been extirpated (Mazanaeva 2001). Rapid recreational urban development in the coastal lowland of the Caspian Sea (Primorskaya lowland) can lead to the extirpation of the last remaining viable populations in this area (Mazanaeva 2001, 2009, 2013, 2021; Mazanaeva and Gichikhanova 2018, 2019, 2020b, 2021).

In Georgia, *T. g. ibera* is threatened by habitat alteration associated with a rapid agricultural expansion, as well as illegal trade in the markets of large cities such as Tbilisi (Chkhikvadze 2009).

In Azerbaijan, there has been a drastic decline in this species since 1930, associated with the intensification of agriculture, and populations only persist in fragmented patches of pristine steppe (Alekperov 1978). In the Zagros Mountains of Iran, uncontrolled fires and occasional severe droughts are negatively impacting this species (Sadegui and Torki 2012).

In Israel, tortoises are mainly threatened by habitat disturbance that is rapid and accelerating in the Mediterranean parts of Israel, where these tortoises are found. All terrestrial vertebrates, including tortoises, are protected by law in Israel, and cannot be caught, killed, or kept as pets. Many regions – especially in the Israeli coastal plain – are being converted to urban areas, with detrimental effects on tortoises (e.g., Perry and Dmi'el 1995). In general, as for most reptiles, habitat loss for agriculture and human habitation is probably the greatest threat to *T. g. terrestris* in Israel (e.g., Dolev and Pervolutzki 2002). Road mortality is prevalent, both on paved and unpaved roads (Dolev and Pervolutzki 2002). Most of the tortoises arriving in the collection of the Steinhardt Museum of Natural History (Tel Aviv University) were run over by vehicles (Meiri, unpubl. data).

Tortoises are often preyed upon by subsidized predators, including birds such as the Hooded Crows (*Covus cornix*) that have proliferated greatly near human habitations. They are also potentially harmed by feral cats and dogs, as well as by wild carnivores that benefit from human refuse and have become more widespread and abundant, such as Golden Jackals and Red Foxes. Wildfires are also a common threat in forested areas (both natural and afforested). Despite the protection by law, tortoises are often collected from the wild and kept for varying periods in homes, kindergartens, schools, and municipal gardens (e.g., Dolev and Pervolutzki 2002), but they are rarely traded.

Conservation Measures Taken. — *Testudo graeca* has been assessed as globally Vulnerable on the IUCN Red List (TFTSG 1996), but this status needs updating. In Europe, it has also been regionally assessed by the IUCN as Vulnerable (van Dijk et al. 2004; Cox and Temple 2009). In most of the countries that encompass the distribution range of *T. graeca*, it is legally protected, but this status is not always associated with long-term conservation plans (Kuzmin 2002; Chkhikvadze 2009; Arsovski and Sterijovski 2019). *Testudo graeca* is also listed on CITES Appendix II (as Testudinidae spp.), helping to regulate international trade.

In North Macedonia, *T. g. ibera* is assessed as Vulnerable on the National Red List and appears on the list of nationally protected wild species (Arsovski and Sterijovski 2019). In Greece, it is protected by the National legislation for the flora and fauna (Council Directive 92/43/EC, May 21st 1992 and in Presidential Decree no. 67, Official Government Gazette 23/A/30–1–81).

Testudo g. ibera occurs within several protected areas of the Greek mainland and islands, such as Natura 2000 Sites: e.g., in Ekvoles potamou Strymona, Limnothalassa Agiou Mama, Stena Rentinas – Evryteri Periochi Spilaio Drakotrypa – Spilaio Lakkia Kai Rema Neromana, Ori Vrontous – Lailias – Erimikes Spilaia Zesta Nera Kai Katarrakto, Kos: Akrotirio Louros – Limni Psalidi – Oros Dikaios

– Alyki – Paraktia Thalassia Zoni, Oros Titaros, Ethniko Thalassio Parko Alonnisou – Voreion Sporadon, Anatoliki Skopelos, Megalo Kai Mikro Livari – Delta Xeria – Ydrochares Dasos Ag. Nikolaou – Paraktia Thalassia Zoni, Delta Nestou Kai Limnothalasses Keramotis – Evryteri Periochi Kai Paraktia Zoni, Oros Stratonikon – Koryfi Skamni, Lesvos: Kolpos Kallonis Kai Chersaia Paraktia Zon, Agios Efstratios Kai Paraktia Thalassia Zoni, Lesvos Kolpos Geras, Elos Ntipi Kai Oros Olympos – Potamos Evergetoulas, Delta Axiou – Loudia – Aliakmona – Evryteri Periochi – Axioupoli, Lesvos: Dytiki Chersonisos – Apolithomeno Dasos, Limnos: Chortarolimni – Limni Alyki Kai Thalassia Periochi, Samos: Paralia Alyki, and Delta Evrou Kai Dytikos Vrachionas.

In the Red Book of threatened animals of Greece, *T. g. ibera* is listed as Least Concern (LC) (Legakis and Maragou 2009), although it is the tortoise in Greece that has the smallest distribution and is the most threatened (Willemsen and Hailey 1989).

In Bulgaria, tortoises have been under increasing legal protection since 1961 (Petrov et al. 2004). Currently they are included in the Biological Diversity Act (2002, latest amendment 2018) and are assessed as Endangered in the national Red Data Book (Beshkov 2015). Implemented measures include a species action plan (Petrov et al. 2004), conservation, education and information campaigns, and anti-poaching efforts. In Bulgaria this species appears in high densities at several sites within the Natura 2000 network, including Rodopi – Iztochni, Sakar, Strandzha, Rupite – Strumeshnitsa, and Nikopolsko Plato. A Tortoise Rehabilitation and Breeding Centre is operated by Gea Chelonia Foundation (Banya, Emine-Irakli Protected Area).

In Romania, populations of *T. graeca ibera* occur in several Natura 2000 Sites, e.g., Dumbrăveni – Valea Urluia – Lacul Vederoasa, Dunărea Veche – Brațul Măcin (arie de protecție specială avifaunistică, SPA), Dunele marine de la Agigea, Ciuperceni – Desa, Delta Dunării (Danube Delta), Pădurea Eseschioi - Lacul Bugeac, Podișul Nord Dobrogean, and Padurea Hagieni.

In Turkey, tortoises have been protected in the context of the Bern Convention, CITES, and the Convention on Biological Diversity. Furthermore, all reptiles including tortoises are included under the national hunting law. Populations of *T. graeca* occur in most of the country except for the eastern Black Sea region. As of 2021, a total of 366,573 ha have been designated as protected areas, which corresponds to 4.8% of the total terrestrial (wetlands excluded) land cover of Turkey.

In the Caucasus, populations of *T. g. ibera* appear in Kavkazskiy Biosphere Reserve in Russia and Gagra, Lagodekhi, Mariamjvar, Pitsundo-Myusserskii, Sagurami, and Vashlovani nature reserves in Georgia, and *T. g. armeniaca* in Khosrov Forest Reserve in Armenia and Ak-Gel, Basut-Chai, Hyrkan, Karayaz, Kyzyl-Agach, Pirkuly, Shirvan, Turian-Chai, and Zakataly nature reserves in Azerbaijan (Kuzmin 2002). In Dagestan in Russia, *T. g. armeniaca* is protected in the Sarykum dunes of the Dagestansky Reserve and in the Samursky National Park. In 2022, a specially protected natural area was created—the Papas coastal natural complex, encompassing the most viable coastal population (Mazanaeva 2001, 2009, 2013, 2021; Mazanaeva and Gichikhanova 2018, 2019, 2020b, 2021).

In Iran, *T. graeca* is assessed as Vulnerable (Safae-Mahroo et al. 2015), but no special conservation measures have been undertaken.

In Israel, tortoises are protected by law and cannot be legally hunted, collected, sold, or kept. They are protected by an extensive array of nature reserves, but the efficacy of this protection has not been evaluated. The presence of *T. graeca* is confirmed in at least 252 national parks and nature reserves throughout the country: e.g., Har Meron Reserve (8096 ha), Ha-Hermon Nature Reserve (7827 ha), Yehuddiya Forest Reserve (7153 ha) and Yehuddiya-Gamla Nature reserve (838 ha), Mount Carmel National Park and Nature Reserve (5333 ha and 3151 ha), Ya'ar Massada National Park (1941 ha), Nahal Qana Reserve (1649 ha), Hadon Shomron Nature Reserve (1558 ha), Holot Nizzanim Reserve (758 ha), Hare Yehuda Nature Reserve (752 ha), Holot Palmahim Reserve (621 ha), Bet Guvrin National Park (513 ha), Nahal Alexander River Reserve (301 ha), Makhtesh Be'eri Nature Reserve (244 ha), HaSharon Park (222 ha), Hayarkon Park (213 ha), and Shitta Malbina Ashdod Nature Reserve (85 ha) (E. Vidan, unpubl. data).

Like other reptiles, their conservation status has not been assessed since 2002. Tortoises are actively protected by the Israeli Nature and Parks authority and there are local plans for releasing individuals illegally kept in captivity back into the wild. Injured and sick tortoises are often brought to a wildlife hospital where they are treated and, if possible, released back into the wild.

Conservation Measures Proposed. — *Testudo graeca* would greatly benefit, like other reptile species, from the creation and maintenance of a network of functional reserves that sustain long-term viable and stable populations of all included subspecies and their genetic diversity, including particular forms/ecotypes or geographically isolated populations. It is also important for the conservation of this species to establish continued and improved long-term monitoring of populations across the range (especially in existing protected areas) and continued monitoring of the wildlife trade for the captive husbandry industry.

Although there are currently a significant number of nature reserves that promote the preservation of a large part of the genetic and phenotypic diversity of the eastern clades of *T. graeca*, additional reserves should be created to protect populations such as those present in the Araxes River valley of Armenia threatened by agricultural expansion (Arakelyan et al. 2011), and in in the Zagros Mountains of Iran, including populations of both *T. g. buxtoni* and *T. g. zarudnyi*. To ensure the long-term preservation of the species in Dagestan, it would be necessary to expand the protected area of the Sarykum dunes in the Dagestan Reserve by including the Narat-Tyube Ridge. We also recommend protecting the natural area in the Kayakent region, including the vicinity of the village of Shalasi (6650 ha) and the Shurdere area (16,380 ha) into the Samursky Reserve, expanding its boundaries by including habitats from the nearby coastal semi-deserts (Mazanaeva 2001, 2009, 2013, 2021; Mazanaeva and Gichikhanova 2018, 2019, 2020b, 2021).

Additionally, further genetic studies are needed to resolve the phylogenetic affinities of all southwest Asian populations (e.g., northern Iraq) and the discongruity of the current subspecies and genetic clades, and to define which groups of clades or taxa should perhaps be recognized as full species, e.g., eastern and western clades and *T. g. zarudnyi* (van der Kuyl et al. 2005; Ranjbar et al. 2022).

Captive Husbandry. — *Testudo graeca* is frequently kept and bred in captivity, with a permanent stock of captive-bred individuals that are generally managed in a regulated way in the European and American hobbyist markets. For instance, there are several breeding farms in Macedonia, which export between 2150 (2016) and 850 (2017) individuals per year, although it cannot be ruled out that these figures may conceal some illegal trade (Ljubisavljević et al. 2011; Arsovski and Sterijovski 2019). Captive breeding is relatively easy in outdoor installations located *in-situ* in native regions and has been reported for most subspecies: *T. g. armeniaca*, *T. g. buxtoni*, and *T. g. terrestris* (Lapid and Robinzon 1995; Taskavak et al. 2004; Taskavak and Türkozan 2004a; Sadegui and Torki 2012; Werner 2016). Anecdotally, it has been reported that *Testudo g. ibera* hybridize in captivity with *T. marginata* (Heimann 1986).

Testudo g. ibera is the most frequently offered subspecies in the hobbyist market, possibly because it is more resistant to thermal extremes than other subspecies of *T. graeca* (Highfield 1990b). Despite this, this species can easily contract fatal respiratory diseases if kept outdoors for long periods in the colder and more humid climates of northern and central Europe (Lambert 1983; Lawrence and Needham 1985).

For the adequate maintenance of this subspecies, it is necessary to maintain a temperature gradient between 26–30°C, with a point of maximum heat of 35–40°C and a nocturnal temperature drop of 10–15°C (Müller 2000; Jepson 2006; Toombs 2013). This subspecies may also require an artificial UVB source in indoor enclosures, operational about 6 hrs a day, for the synthesis of cholecalciferol (calcium metabolism). The floor space of the enclosure should be at least 1.2 × 0.6 m per adult individual. Hibernation is recommended in this subspecies, reducing the temperature to 5–10°C, but not reaching 0°C, and should not last more than 2–3 months (Highfield 1990b; Divers 1996; Müller 2000; Jepson 2006). Exposure to temperatures below 0°C can cause irreversible retinal degeneration and blindness (Divers 1996). Individuals of other subspecies, such as *T. g. terrestris* from southern Turkey, may not require hibernation (RVC Exotics Service 2022). Egg clutches laid in captivity can be artificially incubated at 26–32°C with humidity between 40–80%; males are usually born with temperatures below 28°C and females above 30°C (Divers 1996; Müller 2000; Jepson 2006).

The diet must be varied, but fundamentally herbivorous, and must include vegetable matter rich in cellulose: 75% green leafy vegetables, 15% grated root vegetables, and 10% fruit (Highfield 1990b; Divers 1996). Animal matter, such as dog and cat food, can occasionally be fed, but in excess can cause pyramiding of the shell in juveniles and renal failure in adults (Highfield 1990b; Divers 1996). Juvenile diet of *T. g. ibera* is identical to adults, but needs to provide calcium supplements, e.g., finely crushed cuttlefish shells (Müller 2000). Captive individuals of *T. g. terrestris* (Israel) feed on lettuce, cucumber, dandelion, dichondra, cantalope, banana, tomato, orange, mango, pea, broccoli, spinach, green bean, carrot, celery, flowers, and raw beef (Buskirk 1967).

Current Research. — In Bulgaria, current research includes home range estimation on Sakar Mountain; observation records are continually collected using the SmartBirds.org electronic database.

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