

DE GRUYTER OPEN

# UDC 502.47:598.13(65) HOME RANGE OF THE SPUR-THIGHED TORTOISE, *TESTUDO GRAECA* (TESTUDINES, TESTUDINIDAE), IN THE NATIONAL PARK OF EL-KALA, ALGERIA

R. Rouag<sup>1\*</sup>, N. Ziane<sup>2,3</sup>, S. Benyacoub<sup>2</sup>

<sup>1</sup> Université Chadli Bendjedid. 36100 El Tarf, Algeria

<sup>2</sup> Université Badji Mokhtar. Département de Biologie. BP. 12. El Hadjar. 23000 Annaba, Algeria

<sup>3</sup>Laboratoire de Bio-surveillance environnementale, Département de Biologie, Université Badji Mokhtar 23000 Annaba, Algeria

*E-mail:* rachid\_rouag@yahoo.fr

Home Range of the Spur-Thighed Tortoise, *Testudo graeca* (Testudines, Testudinidae), in the National Park of El Kala, Algeria. Rouag, R., Ziane, N., Benyacoub, S. — Spur-thighed tortoise is a vulnerable species, the local declines of populations require an imperative need for conservation. Research on habitat use is essential for understanding population ecology. To investigate the home range and movement patterns we studied a population which occupies an enclosed area of 30 ha in northeastern Algeria. Studies of movement showed that home ranges were substantially smaller than in Spain. This difference was due to the high trophic availability with significant richness in plants which make part of the diet of the tortoise. The home range varied from 0.287 ha in males to 0.354 ha for females; there was no sexual difference. The males are the most active with a distance of 3.79 m/d. Females and juveniles are respectively about 2.25 m/d and 2.11 m/d. The distance moved each day do not vary significantly by sex and ages. Results from this study are important for establishing conservation strategies for this vulnerable species.

Key words: Algeria, habitat, home range, movement, Testudo graeca, tortoise.

#### Introduction

The Spur-thighed tortoise (*Testudo graeca* Linnaeus, 1758) has a wide distribution in North Africa (Maghreb and Cyrenaica), southern Spain, the Balearic Islands, and in the Balkans east to the Caucasus, Syria, Lebanon, Palestine, Jordan, Iran and Iraq (Ernst, Barbour, 1989; Fritz, Havas, 2007). The species has been studied widely in terms of ecology, demography and geographic variation (Braza et al., 1981; DHaz-Paniagua et al., 1995, 1996 & 2001; Bailey, Highfield, 1996; El Mouden et al., 2001; Van der Kuyl et al., 2002; Ben Kaddour et al., 2005; Rouag et al., 2007). However, *Testudo graeca* habitat and activity patterns have been few studied in northern Africa (Lagarde et al., 2008; Lagarde et al., 2012). So, the aim of this work is to study the modes of exploitation of the habitat by the species in a dune maquis in the National Park of El Kala. The dune maquis despite its simplicity to other formations such as cork oak contains 60 % of the Reptile of the park. It is the richest with 10 species belonging to Testudines, Ophidia and Sauria. For reptiles, the open environment is an ideal ground to the extent that it provides spaces necessary for thermoregulation and diet, and bushy vegetation that can be used to escape predators (Greenberg, 2001). Many animals can survive food or water shortage, at least in the short term, but none can afford even short-term overheating (Vickers et al., 2011). These habitats provide access to optimum temperatures (Webb, Shine, 1998), but they are limited by the degree of openness of vegetation (Pringle et al., 2003).

<sup>\*</sup>Corresponding author

The Spur-thighed tortoise, *Testudo graeca*, recorded a decline phase in its range, the reasons for this decline are many, but they are mainly related to the degradation and changes in habitat due to human activities (Pringle et al., 2003; Rouag, 2015). The opening of new roads and the expansion of existing ones, fragment habitats increase their crushing mortality rates. Forest fires can cause real devastation, especially in wooded areas. This factor becomes more and more threatening in recent years with global warming and increased fire frequency. Modern agriculture is another threat as a direct way by crushing by tractors and other machinery, and also by the use of chemicals (pesticides, herbicides, etc.) and indirectly, by clearing more natural habitats of tortoises (Rouag, 2015). In this context, we must be able to better understand the ecology of this species, especially as species conservation status is an important factor in assessing the importance of habitats in which they live there. This status also represents an important tool when it comes to establishing priorities for conservation.

#### Materials and methods

#### Study area

This study was carried out in the National Park of El Kala, in north-eastern Algeria, situated between 36° 49′ 01″ north and 8° 24′ 47″ East. Overall, the national park has a surface of 78 400 ha, and is characterized by a varied terrain with lakes, marshes and hilly territories, covered with relatively dense vegetation (De Belair, 1990). The climate was Mediterranean (Seltzer, 1946); rainfall was moderate, and strongly concentrated during the winter months: total annual rainfall was about 630 mm, and the mean monthly rainfall was about 52 mm. The study site (around Boumalek) was characterized by a Mediterranean maquis vegetation type growing on a sandy soil; the main vegetation cover was due to the Mediterranean dwarf palm *Chamaerops humilis*, but the site was also strongly cultivated (mainly cereals, peanuts, etc.). The mean height of the bushy layer was 32.4 cm, and the mean bushy vegetation coverage was 19.4%; the mean height of the grassy layer was 2.3 cm, and the average grassy vegetation coverage was 70 %.

#### Research protocol

This study was carried out during a seven-month period, i. e. between March and September, in 2004. The surface of the study site was approximately 30 ha. The tortoises were searched for by random walks throughout the study area. Once captured, they were marked individually by carapace scale notching (Bury, Luckenbach, 1977; Luiselli, 2003), measured for carapace length and body weight and then set free unharmed to the site of capture. The carapace length was measured by a digital caliper (precision  $\pm$  0.1 mm) with the same measure-

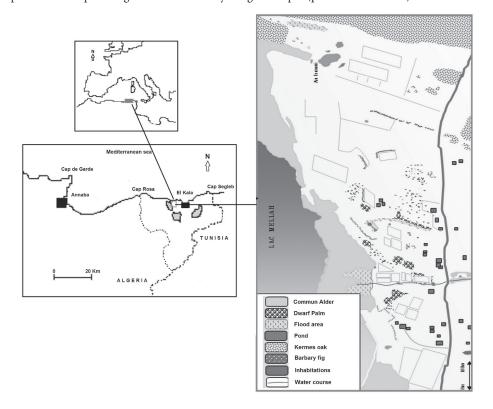


Fig. 1. Location of the study site in the National Park of El Kala, in north-eastern Algeria.



Fig. 2. View of the study area with different habitats.

ment criteria of Stubbs (Stubbs, Swingland, 1984). The body mass of the tortoises was measured by a digital balance (precision  $\pm$  1 g). Sex was determined by examining the plastron concavity and the tail length (which is much longer in the males than in the females). Sex was established only in individuals with a carapace length > 80 mm; the smaller specimens were considered as a juvenile. Age determination of each captured tortoise was done by growth annuli counts on the shell, one growth annulus being added each year (Saint Girons, 1965; Castanet, Cheylan, 1979; Germano, Bury, 1998).

#### Habitat Description

The site as previously described is presented as a rural habitation type with cultivated plots and grass vegetation composed with the Mediterranean dwarf palm (*Chamaerops humilis*). At the west of the site, we note the presence of common alder (*Alnus glutinosa*) along the banks of Lake Mellah. The northern part is limited by the Kermes oak (*Quercus coccifera*) on dune soil (figs 1, 2). We also note several rows of Barbary Fig (*Opuntia ficus-indica*). Once the animal is located the state of the surrounding vegetation is raised. We estimated each observation of individuals within 5 meters of the place of observation. The average recovery (%) of vegetation for different shrub was noted. The tortoise distribution map was made from the aggregated data of all tortoises contact throughout the season (100 observations).

#### Home range estimation

The home range is generally defined as the area occupied by an animal to develop normal activities of any kind. MCP methods (minimum convex Polygon) consist of connecting the points of extreme locations to draw a polygon and then calculate its area (White, Garrott, 1990). To do so, we have recorded the GPS coordinates of the locations of tortoises observed during each output in the Map Source software (version 6.16.3). The estimate of the home range was made only from 7 tortoises (2 females and 5 males) each one recaptured three times during the working season. The material used for the geo-location of contact points with the tortoises is a GPS Garmin 72 H. The data are then transferred to (Google earth pro. version 7.0.2.8415) in order to calculate the areas of the MCP. We have followed the method used by Turner (Turner et al., 1969) for the bias in the sample size with a logarithmic equation to normalize the data set. The playground which results is the MCP corrects of the home range of the animal. The formula used is:

(Area of MCP) / (0.257 x ln (n) - 0.31),

where n = number of locate points (Barrett, 1990). This method corrects the bias in the sample size.

#### Daily movement distance

Daily travel distance (m/d) was calculated on 17 tortoises (7 males, 7 females and 3 juveniles) recaptured during the study period. The distance traveled per day is the distance between two points of capture and recapture (meters) on the crossing time (days).

#### Statistical analysis

The differences between males and females in the home range were tested with *t*-test. The differences between the daily distance movements among the tree groups were tested with t-test. Normality was assessed using a Shapiro-Wilk test. The relationships between daily movement distance and morphological parameters (weight and length) were assessed by Spearman's rank correlation coefficient. All statistics were computed by SPSS (version 11.0) PC package, with all tests being two-tailed and a set at 5 %. Means are followed by  $\pm$  standard deviation (Sd).

Result

## Habitat Description

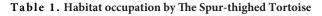
For analyzing the habitat of the spur-thighed tortoise we based on the superimposition of the home ranges of the recaptured tortoises and vegetation distribution in the study area. The analysis of the home range of the seven tortoises revealed three major types of habitats regularly exploited during the active season. These habitats are represented by grasslands with 65 % of covering and the Mediterranean dwarf palm with 33.57 %. The common alder is few used by tortoises (table 1).

Analysis of the distribution map shows that it is not done regularly throughout the site. In fact, we can see the existence of four cores composed of 20 individuals and a small of 10 individuals. The affinities between the presence of tortoises and site vegetation structure were developed by a superposition of the two layers (fig. 3). There is a close relationship between the distribution of tortoises and the presence of dwarf palm (*Chamaerops humilis*) in the study area. In fact, *C. humilis* is the ideal habitat for tortoises in this environment where it plays a dual role in thermoregulation and also for shelter.

## Estimation of home range

The coordinates of the locations of the tortoises have been marked by a GPS. By connecting the dots for each individual, the software gives us the home range size. Using

Habitats, %	Mean	± Sd	Min	Max
Dwarf palm	33.57	15.47	10	50
Grasslands	65	16.58	50	90
Common alder	1.43	3.78	0	10



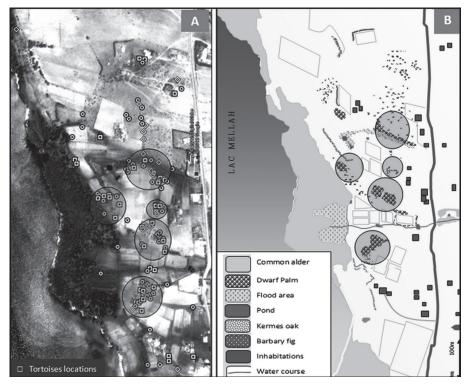


Fig. 3. Tortoises locations (A) in relation to Dwarf palm distribution (B) on the study site.

Sex	Mean	± Sd	Min	Max
males (n=5)	0.287	0.060	0.191	0.621
females (n=2)	0.354	0.342	0.112	0.596

Table 2. Home range (ha) for 07 tortoises (calculated by MCP)

the formula of the area of the corrected Turner field is obtained, which corresponds to the area theoretically exploited by the tortoise for all those biological activities.

The home range corrected for the males ranged from 0.191 ha (1910 m<sup>2</sup>) to 0.621 ha (6210 m<sup>2</sup>) with an average value of 0.287 ha (2870 m<sup>2</sup>). For females the corrected home

Sex and age	Carapace Length, mm			Carapace Weight, g			Movement dis- tance, m			Number of days			Daily movement, m/day							
group	Mean	± Sd	Min	Max	Mean	$\pm Sd$	Min	Max	Mean	$\pm Sd$	Min	Max	Mean	$\pm Sd$	Min	Max	Mean	$\pm Sd$	Min	Max
$\frac{\text{males}}{(n=7)}$	143.74	10.73	130.28	161.07	664.57	144.37	740	860	70	57.9	20	174	22.29	10.06	ŝ	31	3.79	2.9	0.67	6
females $(n = 7)$	148.95	35.83	76.82	170	922.5	418.03	116	1275	71.5	73.42	9	195	31	9.34	14	41	2.25	2.20	0.41	5.74
juveniles (n = 3)	58.68	4.12	55.83	63.4	48.33	1.53	47	50	52	45.30	10	100	28.67	8.08	24	38	2.11	1.96	0.26	4.17

Table 3. Morphmetrical data and daily movement distance (Mean  $\pm$  Sd, range)

range is larger than the males with a mean value of 0.354 ha (3540 m<sup>2</sup>) (table 2). Males and females do not differed significantly in terms of both home range (p = 0.758 > 0.05, t = 0.324, df = 5 at *t*-test).

## Daily movement distance

The frequency distributions of average distance traveled per day matched normal distributions (Shapiro-Wilk normality tests: males: W = 0.902, p = 0.349; females: W = 0.848, p = 0.152, juveniles: W = 0.992, p = 0.834; adults: W = 0.895, p = 0.114).

The following table shows the calculated values of the distance traveled every day by the recaptured individuals. The males are the most active with an average distance traveled per day (3.79 m/d). Females and juveniles are respectively about 2.25 m/d and 2.11 m/d (table 3). The application of the *t*-test shows no significant difference between the daily distance movement between males and females (p = 0.310 > 0.05, t = -1.064, df = 11) and between adults and juveniles (p = 0.562 > 0.05, t = -0.593, df = 14).

We have verified that the morphological parameters are related to the distances traveled by the tortoises. In females, there is no correlation between the daily movement distance and the length of the carapace r = 0.482 (p = 0.333) and weight: r = 0.433 (p = 0.392). In males also, there is no correlation between the daily movement distance and the length of the carapace r = -0.182 (p = 0.695). There is no correlation with the weight: r = -0.064(p = 0.891).

## Discussion

Understanding the use of space and movement patterns of a species in its home range was the subject of numerous studies. The use of the space of a species is very important for biologists because it provides valuable insight on the specific needs of an organism (Kernohan, 2001). The home range is related to reproduction and looking for a partner, especially in male tortoises, or selection of the nesting site in the female tortoise (McRae, 1981; Eubanks, 2003). The estimated ranges may vary depending on a number of factors, including the method of estimation, the number of locations, the sampling frequency, the duration of the study, the distribution of point observation of software (Mitchell, 2011).

The analysis of home range based on monitoring of seven tortoises (05 males and 02 females) highlights three main types of habitats regularly exploited during the active season. These environments are represented by common alder, dwarf palm and grasslands. The three groups play a complementary role in modes of chelonian activities.

The home range of the tortoise is 0.3 ha; it is small than those studied in Murcia with 1.7 ha (Giménez, 2004) and also in Doñana where Andreu (1987), estimates that the home range is 2.96 ha after following three males and three females. In central Jbilet (Morocco) tortoises show a small home range 0.2 ha (Slimani, 2002). This may be related the rugged nature of the terrain and also high temperatures levels especially in summer, this site is characterized by an arid climate (table 4).

This small home range can be explained by the high trophic availability in our site with significant richness in plants which make part of the diet of the tortoise; especially Poaceae (Cynodon dactylon and Hordeum murinum) and Fabaceae (Trifolium sp.) which cover more than 75 % of the area (Rouag, 2008). The presence of dwarf palm (Chamaerops humilis) on site provides an important refuge for thermoregulation and shelter against predators. Thus, tortoise does not venture far in search of food. Our results are comforted by those of (Mazzotti et al., 2002) who attributed the Larger home ranges of Testudo hermanni which occur in northern Italy (4.6 ha in males and 7.4 ha in females) to food scarcity in this area. The high selection for cultivated land could also be due to their role in laying eggs, as is the case for other populations of Testudo graeca (Stubbs, Swingland, 1984). The vegetation structure is also an important factor because it influences microhabitats by controlling the penetration of the sunlight, which affects the microclimate at the soil. Our results have conservation implications that are potentially valuable to this rare species. Increasing the number of habitats containing Chamaerops humilis in open habitat with low vegetation cover such as agrosystem provide relatively ideal habitats for the tortoise. Their management and conservation is an important tool in reptile conservation strategies. Thus, any change in the availability of open habitats could directly influence the herpetological diversity.

Estimating the distances traveled by the tortoises was done by the accumulated observations along the active season. It would be interested to do an analysis of the distances traveled by month to see if there is a variation between the sexes and ages. Our study did not show significant differences in distances traveled by sex and age. Other studies such as (Lagarde, 2008) and (Díaz-Paniagua, 1995) show no difference in moving between males and females.

## Conclusion

The Spur-thighed tortoise exists in a great geographical area in Algeria; This enable it to have great opportunities to maintain itself, but the main threats of reptiles and tortoises,

Sites	Total	Males	Females	References
Doñana (Spain)	3.0	3.37	2.55	Andreu (1987)
Murcia (Spain)	1.7	2.56	1.15	Gimenez et al. (2004)
Jbilet (Morocco)	0.2	0.17	0.24	Slimani et al. (2002)
El Kala (Algeria)	0.3	0.28	0.35	Current study

Table 4. Estimated home range for different populations of Testudo graeca, ha

in particular, are the increasing of the fragmentation and destruction of their habitats. The opening of new roads and the enlargement of existing ones inside the National Park of El Kala increase their mortality by crushing especially because of their slow movement. Modern agriculture is another threat; in a direct way, by crushing by tractors and other devices and also by the use of chemicals (pesticides, herbicides, etc.); and indirectly, by clearing the natural habitats of tortoises. Overgrazing is an additional threat; tortoises that are herbivorous are challenged in their environments by cattle that exploit the same food resources. The collecting of tortoises to support the trade is one of the most significant threats. In Algeria, the Spur-thighed tortoise is protected by the law on the protection of endangered animal species. In this text are identified the species of wildlife threatened and which are therefore the subject of measures of protection. The problem of conservation resides mainly in the application of this regulation by the authorities. The conservation of the habitat of this species is the fastest and safest way to maintain the species. This involves encouraging the local actors (private landowners, farmers, protected areas managers, etc.) to take into account the protection of the Spur-thighed tortoise on the territories they manage.

We thank José D. Anadón, for his valuable corrections and suggestions on the manuscript an anonymous reviewer for helpful comments. We also thank the Director of the National Park of El Kala for licenses to capture tortoises.

#### References

- Andreu, A. C. 1987. Ecología y dinámica poblacional de la tortuga mora, Testudo graeca, en Doñana. Tesis Doctoral. Univ. Sevilla.
- Bailey, J. R., Highfield, A. C. 1996. Observations on ecological changes threatening a population of *Testudo* graeca graeca in the Souss Valley, southern Morocco. *Chel. Cons. Biol.*, **2**, 36–42.
- Ben kaddour, K., El Mouden, E. H., Slimani, T., Lagarde, F., Bonnet, X. 2005. Dimorphisme sexuel et cinétique de croissance et de maturation chez Testudo g. graeca, dans les Jbilets Centrales, Maroc. *Rev. Ecol.*, **60**: 265–278.
- Braza, F., Delibes, M., Castroviejo, J. 1981. Estudio biométrico y biolygico de la tortuga mora (*Testudo graeca*) en la Reserva Biolygica de Docana, Huelva. Docana. *Acta. Vertebr.*, **8**, 15–41.
- Bury, R. B., Luckenbach, R. A. 1977. Censusing desert tortoise populations using a quadrat and grid location system. *Proc. Symp., The Desert Tortoise Council*, 169–178.
- Castanet, J., Cheylan, M. 1979. Les marques de croissance des os et des écailles comme indicateur de l'âge chez *Testudo hermanni* et *Testudo graeca* (Reptilia, Chelonia, Testudinidae). *Can. J. Zool.*, **57**, 1649–1655.
- De Belair, G. 1990. Structure, fonctionnement et perspectives de gestion de quatre complexes lacustres et marécageux (El Kala, Est algérien). Thèse de Doctorat, Université du languedoc, 1–193.
- Díaz-Paniagua, C., Keller, C., Andreu, A. C. 1995. Annual variation of activity and daily distances moved in adult Spur-thighed tortoises, *Testudo graeca*, in southwestern Spain. *Herpetologica.*, **51**, 225–233.
- El Mouden, E., Slimani, T., Ben Kaddour, K. 2001. Croissance et dimorphisme sexuel chez la tortue mauresdque (*Testudo graeca graeca* L., 1758). Proceeding of the international congress on Testudo Genus. *Chelonii*, 325–330.
- Ernst, C. H., Barbour, R. W. 1989. Turtles of the World. Smithsonian Institution Press, Washington D.C. 1–313.
- Eubanks, J., Ott, M., William, K., Guyer, C. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). *Herpetologica.*, **59**,311–321.
- Fritz, U., Havas, P. 2007. Checklist of chelonians of the world. Vertebrate Zoology (Dresden), 57 (2), 149-368.
- Germano, D. J., Bury, R. B. 1998. Age determination in turtles: Evidence of annual deposition of scute rings. Chel. *Cons. Biol.*, **3**, 123–132.
- Giménez, A., Esteve, M. A., Pérez, I., Anadón, J. D., Martínez, M., Martínez, J., Palazón, J. A. 2004. *La tortuga mora en la Región de Murcia*. Conservación de una especie amenazada. DM Ed. Murcia.
- Greenberg, C. H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. *For. Ecol. Manage.*, **148**, 135–144.
- Kernohan, B. J., Gitzen, R. A. et Millspaugh, J. J. 2001. Analysis of animal space use and movements in Radio tracking and animal populations. Academic Press, San Diego, 125–166.
- Lagarde, F., Guillon, M., Dubroca, L., Bonnet, X., Ben Kaddour, K., Slimani, T. 2008. Slowness and acceleration: a new method to quantify the activity budget of chelonians. *Anim Behav.*, **75**, 319–329.
- Lagarde, F., Louzizi, T., Slimani, T., El Mouden, H., Ben Kaddour, K., Moulherat, S., Bonnet, X. 2012. Bushes protect tortoises from lethal overheating in arid areas of Morocco. *Environ Conserv.*, **39**, 172–182.

- Luiselli, L. 2003. Comparative abundance and population structure of sympatric Afrotropical tortoises in six rainforest areas: the differential effects of "traditional veneration" and of "subsistence hunting" by local people. *Acta Oecol.*, **24**, 157–163.
- Mazzotti, S., Pisapia, A., Fasola, M. 2002. Activity and home range of *Testudo hermanni* in Northern Italy. *Amphibia–Reptilia*, **23**, 305–312.
- McRae, W. A., Landers, J.L., Garner, J. A. 1981. Movement patterns and home range of the Gopher Tortoise. *American Midland Naturalist*, **106**, 165–179.
- Mitchell, B. R. 2011. Comparison of programs for fixed kernel home range analysis, 5.4. Available from: http:// www.uvm.edu/~bmitchel/Publications/HR\_Compare.pdf
- Pringle, R. M., Webb, J. K., Shine, R. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology*, **84**, 2668–2679
- Rouag, R., Benyacoub, S., Luiselli, L., El Mouden, E. H., Tiar, G., Ferrah, C. H. 2007. Population structure and demography of an Algerian population of the Moorish tortoise, *Testudo graeca. Anim. Biol.*, 57, 267–279.
- Rouag, R., Ferrah, C., Luiselli, L., Tiar, G., Benyacoub, S., Ziane, N., El Mouden, E. H. 2008. Food choice of an Algerian population of the spur-thighed tortoise, *Testudo graeca*. *African Journal of Herpetology*, **57**, 103–113.
- Rouag, R. 2015. Approche fonctionnelle de l'écologie de deux espèces de Reptiles Lacertidés insectivores (Psammodromus algirus et Acanthodactylus erythrurus) et d'un reptile chélonien phytophage (Testudo graca graeca), dans un maquis dunaire du parc national d'El-Kala (Wilaya d'El-Tarf). Thèse de Doctorat, Université Chadli Bendjedid, El Tarf, 165 p + annexes.
- Saint Girons, H. 1965. Les critères d'âge chez les reptiles et leurs applications à l'étude de la structure des populations sauvages. *Rev. Ecol.*, **4**, 342–357.
- Seltzer, P. 1946. Le climat de l'Algérie. Impr. «La Typo-litho» & J. Carbonel, 1–219.
- Slimani, T., El Mouden, E. H., Ben Kaddour, K. 2002. Structure et dynamique de population de *Testudo graeca* L., 1758 dans les Jbilets Centrales, Maroc. *Chelonii*, **3**, 200–207.
- Stubbs, D., Swingland, I. R. 1984. The ecology of the Mediterranean tortoise (*Testudo hermanni*): a declining population. *Can. J. Zool.*, **63**,169–180.
- Turner, F. B., Lannom, J. R., Medica, P. A., and Hoddenbach, G. A. 1969. Density and composition of fenced populations of leopard lizards (*Crotaphytus wislizenii*) in southern Nevada. *Herpetologica*, 25, 247–257.
- Van Der Kuyl, A. C., Ballasina, D. L., Dekker, J. T., Maas, J., Willemsen, R. E., Goudsmit J. 2002. Phylogenetic relationships among the species of the genus *Testudo* (Testudines: Testudinidae) inferred from mitochondrial 12D rRNA gene sequences. *Mol. Phyl. Evol.*, 22, 174–183.
- Vickers, M., Manicom, C., Schwarzkopf, L. 2011. Extending of the cost-benefit model of thermoregulation: high temperature environments. *The American Naturalist*, **177**, 452–461.
- Webb, J. K., Shine, R. 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biol. Conserv.*, **86**, 233-242.
- White, G. C. and Garrott, R. A. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, CA, 1–383.

Received 25 January 2017 Accepted 18 March 2017