

THE ROLE OF RELIEF IN LOCAL ABUNDANCE PATTERNS OF THE SPUR-THIGHED TORTOISE *TESTUDO GRAECA GRAECA* IN SOUTH-EAST SPAIN

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We searched for patterns in the local abundance of *Testudo graeca graeca* with respect to relief characteristics in south-east Spain. The detection of tortoises during linear transects, in sampling plots and through fortuitous observations was used to examine distribution in relation to aspect and to topographic position at two different local scales. Both aspect and run-off gradients produced spatial patterns in the local abundance of *T. g. graeca*. These patterns are discussed with regard to the key conditions and resources for the species (solar radiation, food and nesting sites). At both scales tortoises were more abundant on north-west facing slopes, where solar radiation levels are assumed to be moderate to high, and where there are probably plenty of food resources. The apparent avoidance of north-east facing slopes, despite an abundance of food, suggests that tortoises may not be able to thermoregulate adequately in these areas and that thermoregulation may be the most important requirement for the species. Valley bottoms, mainly occupied by non-irrigated crops, were also selected. Therefore, our results suggest that there is a spatially aggregated population structure at a local scale that is caused by factors associated with relief.

Key words: aspect gradient, Chelonia, ecology, run-off gradient, topography

INTRODUCTION

The spur-thighed tortoise *Testudo graeca graeca* L. 1758 is a medium-sized terrestrial tortoise that mainly inhabits semi-arid environments. It has a westerly circum-Mediterranean distribution and the largest European population is spread over ca. 3000 km² in south-east Spain. In this area, the environmental factors that explain its distribution at a regional scale here are well known (Anadón *et al.*, in press), *T. g. graeca* occurs in semi-arid shrub habitats linked to mountain systems and is absent from large plains and basins. In the region of Murcia, which encompasses 60% of the range of the species in southeast Spain, there are 17 different geographical population units, ranging from 1 to 300 km², which are mainly associated with mountain systems and their piedmonts (Giménez *et al.*, 2001). However, very little is known about the spatial ecology of the species at a local scale.

During this study we searched for patterns in the local abundance of the spur-thighed tortoise with regard to the principal gradient types - topographic (runoff) and aspect - associated with relief. The topographic gradient is determined by the existence of an exporter zone (at the top) and an importer zone (at the bottom), between which there are important spatial differences in soil composition and moisture and, as a result, in vegetation and productivity (Forman & Godron, 1986). Different compass orientations give different levels of solar radiation and, therefore, microclimatic variations related to temperature and moisture levels occur, which can have

important consequences on both vegetation and productivity. Aspect is the variable that best explains variations in vegetation composition and soil moisture at a local scale in the semi-arid shrublands present in the south-east of the Iberian peninsula (Tong, 1989; Ferrer Castán, 1994). Terrestrial tortoises are ectothermic herbivores and have limited mobility; they may therefore show pronounced spatial patterns caused by environmental heterogeneity associated with local relief features. Their thermoregulatory and trophic strategies may promote habitat selection processes, which thus create spatial patterns in habitat use and local abundance.

MATERIALS AND METHODS

STUDY AREA

Our study was carried out in the Biological Reserve "Las Cumbres de la Galera" in the Sierra de la Carrasquilla (Murcia, Spain), managed by the Foundation 2001 Global Nature. It has a mean annual rainfall of 295 mm and a mean annual temperature of between 18-19°C (Ramírez, 1990). The altitudinal range of the reserve is 515-655 m a.s.l and it is characterised by a system of valleys (ramblas) with hillsides of moderate-to-steep gradients. Inside the reserve (70 ha), we established a study area of 29.7 ha that included three slopes facing in different directions belonging to two perpendicular watersheds (Fig. 1). The vegetation present in the study area includes *Anthyllis cytisoides* shrubland, patches of *Stipa tenacissima* and mixed shrubland of mainly *Rosmarinus officinalis*, *Artemisia* ssp., *Thymus* spp. and *Cistus* spp. The *Anthyllis cytisoides* shrubland is a secondary growth community that is usually caused by the abandonment of marginal

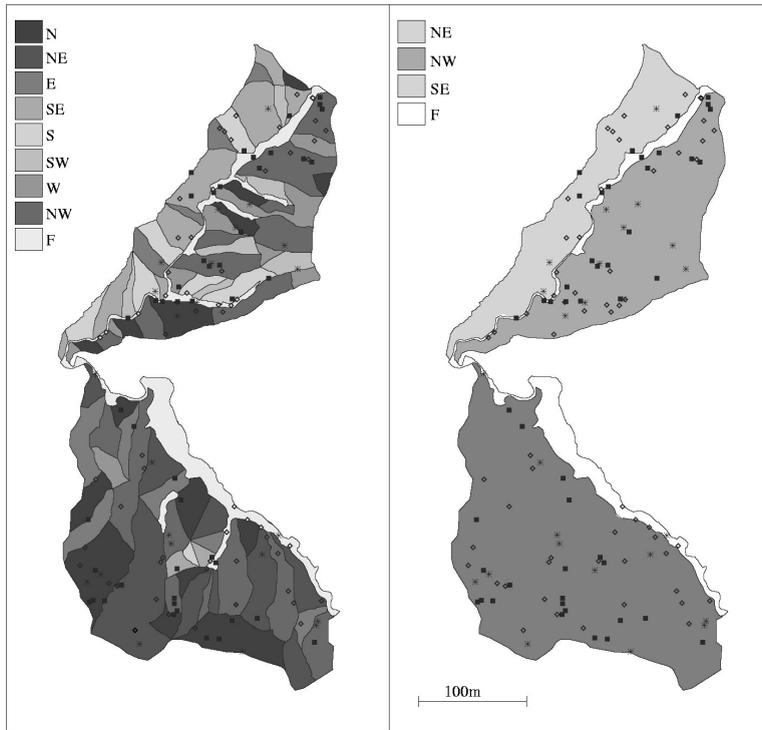


FIG 1. Orientation of slopes in the study area at large (left) and small scales (right) and locations of tortoises (squares = males, diamonds = females, asterisks = immatures).

farmland. In fact, part of the study area was cultivated until 1960, and there are still some small fields of non-irrigated crops in the bottom of the ramblas. The area is considered to be optimum habitat for the species according to habitat quality models developed at a regional scale (Giménez *et al.*, 2001). Capture-recapture studies in the study area have estimated a density of 16 tortoises/ha (authors, unpublished data). This value is high when compared with other *T. g. graeca* populations (Andreu *et al.*, 2000; Slimani *et al.*, 2002).

RELIEF CHARACTERISATION

We mapped aspect and topographic position with a GIS (GRASS 5.0, <http://grass.itc.it/>). We used water-

TABLE 1. Number of patches (*n*), percentage of the study area occupied by each one of the classes of the compass orientation variables, and number of tortoises located (NTOR), at the large and small scale.

Classes	Large scale			Small scale		
	<i>n</i>	%	NTOR	<i>n</i>	%	NTOR
N	-	-	-	14	16	27
NE	1	50.42	59	10	17.35	14
E	-	-	-	10	8.19	6
SE	1	26.39	15	10	9.72	11
S	-	-	-	7	5.7	5
SW	-	-	-	6	3.65	1
W	-	-	-	9	5.67	8
NW	1	15.25	49	17	24.01	41
Flat relief (F)	1	7.94	13	2	9.71	23

sheds as mapping references at two different scales. In species-habitat relationships, different scales of observation may lead to different patterns and processes (Wiens *et al.*, 1987; Wiens, 1989; Turner, 1989) and the detection of a given pattern will depend, partly, on the use of an appropriate scale. For this reason, we employed two different scales of observation. Third-order watersheds were used as reference for large-scale mapping, while first-, second- and third-order watersheds were used as references for small-scale mapping. The large scale reflected the main slopes of the study area, while the small scale reflected the different more minor slopes, which form part of the major slopes. The use of watersheds as references for scale mapping is an objective criterion for defining boundaries and yields two scales, which are strongly related to the natural organisation of landscapes.

Aspect was described by two variables linked to the two different scales (Fig. 1 and Table 1). Within these two variables there were nine possible classes corresponding to the points of the compass: N, NE, E, SE, S, SW, W, NW and F (flat relief). Four classes only were present at the large scale (SE, NW, NE and F), each one linked to one major slope plus the valley bottoms (F). The small scale (small slopes) exhibited all nine classes. Mean patch size for the slopes (valley bottoms included) at the large scale was 7.43 ha, while mean patch size for the slopes at the small scale was 0.35 ha.

In order to describe the topographic position on each slope we divided slopes at both large and small scales into three parts (Fig. 2): bottom (gully), middle (slope) and top (ridge). At the small scale, the top was defined as a buffer zone of 10 m wide around the first-, second-

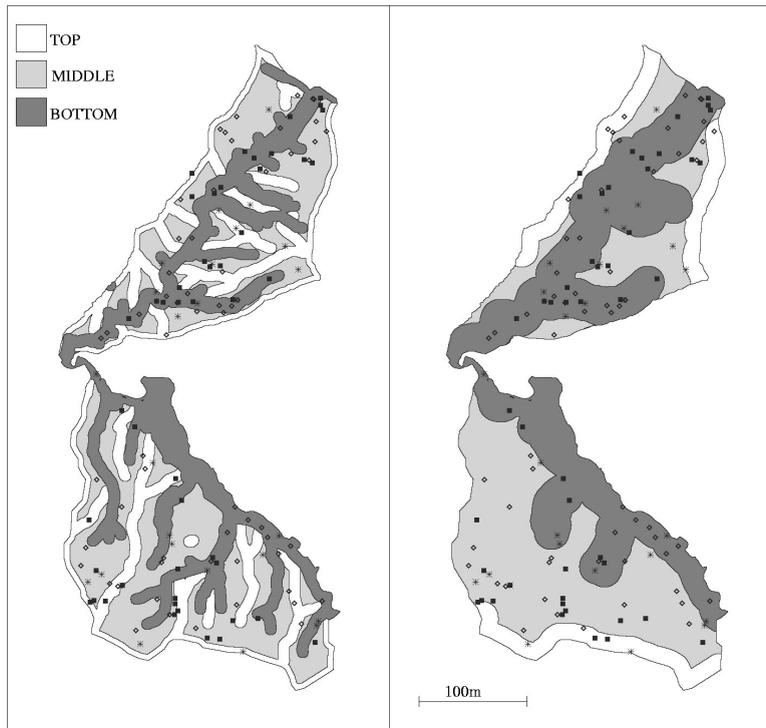


FIG 2. Parts of the slope in relation to the topographic (run-off) gradient in the study area at large (left) and small scales (right) and locations of tortoises (squares = males, diamonds = females, asterisks = immatures).

and third-order watersheds. The bottom was defined as a buffer zone of 10 m wide around the valley bottom (first-, second- and third-order valleys). The middle sector was defined as being that part of the slope that was not contained either within the top or the bottom sectors. At the large scale, linked to the major slopes, we constructed three variables using a buffer-zone width of 20, 30 and 40 m respectively.

SURVEYING METHODS

For the habitat selection analysis, we used the detection of tortoises during linear transects, surveys in sectors and fortuitous observations from other studies in the area. The area was intensively surveyed from the end of February to June, and in September and October, in hours of maximum activity for the species (at midday or in the morning, depending on the period of the year) (Andreu *et al.* 2000; Pérez *et al.* 2002). For sampling by sectors, we divided the study area into twelve sectors of equal area. All the sectors were surveyed simultaneously for two hours by three observers per sector. This sampling methodology was carried out eight times between 1997 and 2000. In 1997 we carried out nine linear transects, covering the study area evenly. The third group of tortoise locations were fortuitous sightings arising from vegetation sampling campaigns and surveys of tortoises for other purposes (Anadón, 2002). We recorded most locations of tortoises with a GPS and if a GPS was not available, sightings were located on aerial photographs (scale 1:5000).

Individuals were classified as males, females or immature. We considered immature animals to be less than seven years old (Andreu *et al.*, 2000). We used the

number of scute rings as an age estimator (Castanet & Cheylan, 1979; Germano & Bury, 1998). Males and females were distinguished visually since clear morphological differences exist (Andreu & López-Jurado, 1998).

DATA ANALYSIS

We compared the observed distribution of tortoises with a random distribution of variables related to aspect and topographic position using a χ^2 test. Recaptures were not taken into account during the analyses. If there were significant differences between classes ($P < 0.05$), an analysis of subdivided contingency tables was performed in order to assess the classes that were responsible for the differences (Zar, 1984). In this second analysis, all pairwise differences between adjacent classes were tested by searching for the groups of classes with minimal intra-group differences and maximal differences between groups, as expressed by their two values. In the variables related to the aspect gradient, the class referring to flat areas (F) was not included in any group and was considered in itself as a separate group since it does not belong to the circular aspect gradient. Analyses of the variables with regard to aspect at the small scale were made for the whole study area and for each major slope (orientation at the large scale) separately in order to detect whether the preferences for orientation at the small scale (small slopes) also held for the differing major slopes. These analyses were made for all individuals and for males and females separately. We also performed a previous test comparing the distribution of males and females in relation to each one of the environmental variables.

TABLE 2. Relevant results of the χ^2 test and partial χ^2 test for compass orientations at the large scale.

Classes	df	χ^2	P
NE, NW, SE and F	3	8.16	0.0429
NE, SE	1	0.36	0.5479
(NE+SE), NW and F	2	7.317	0.0258

RESULTS

ASPECT GRADIENT

A total of 136 locations - 47 males, 61 females and 28 immatures - of different tortoises were made (Fig 1). The number of locations of tortoises per unit area varied substantially from one major slope to another (Table 1). Locations per unit area on the major north-west facing slopes were twice as frequent as those on the major southeast-facing slopes. There was a significant difference in the distribution of tortoises among aspect classes (Table 2). Analysis of subdivided contingency tables showed that tortoises were more abundant in the north-west facing slopes in comparison with flat areas (valley bottoms) and the group made up of north-east and south-east facing slopes (Table 2). This variable did not give any differences for males as opposed to females. At the small scale, there were also significant differences between classes (Table 3). Three homogeneous groups arose from the analysis of subdivided contingency tables: one group consisted of west, north-west and north facing slopes; another of north-east, east, south-east, south and south-west facing slopes and a third was made up of flat areas (hereafter, NW group, SE group and F). The SE group showed the least number of locations of tortoises. There were no significant differences between the NW group and F, whereas there was a significant difference between F and all the other compass orientations grouped together (Table 3). The resulting abundance ranking is: F NW group > SE group.

More tortoise locations were found in the NW group than in the SE group when we compared these two groups separately within the NW and NE major slopes. No analysis was carried out on the SE major slope group since the NW group was not represented.

Finally, χ^2 tests did not detect differences in the distribution of males and females in relation to aspect, neither at the large nor at the small scale.

TABLE 3. Relevant results of the χ^2 test and partial χ^2 test for compass orientation at the small scale.

Classes	df	χ^2	P
N, NE, E, SE, S, SW, W, NW and F	8	21.5	0.006
(N+NW+W), (NE+E+SE+S+SW) and F	2	19.6	0.000
N, NW and W	2	0.2	0.882
NE, E, SE, S and SW	4	2.5	0.636
(N+NW+W) and F	1	2.2	0.135
(N+NW+W) and (NE+E+SE+S+SW)	1	12.5	0.000
(NE+E+SE+S+SW) and F	1	17.1	0.000

TABLE 4. Results of the χ^2 test of variables referring to 'position on the slope at small and large scales. The variable at the large scale is the one with buffer-zone width of 20 m, since it is the only one that yielded significant differences among its classes. T=Top part, M= middle, B=bottom.

	Large scale			Small scale		
	df	χ^2	P	df	χ^2	P
T, B and M	2	6	0.050	2	5.98	0.050
T and B	1	5.0	0.026	1	5.89	0.015
(T+B) and M	1	0.6	0.446	1	0.42	0.516
T and M	1	1.9	0.163	1	3.69	0.055
(T+M) and B	1	4.2	0.039	1	2.66	0.103
B and M	1	3.0	0.083	1	0.4	0.527
(B+M) and T	1	2.8	0.091	1	7.43	0.006

TOPOGRAPHIC POSITION ON THE SLOPE

For the topographic position at the large scale and for all individuals there were significant differences among the top, the middle and the bottom parts when the buffer-zone width was 20 m (Table 4), but not when the buffer-zone width was 30 or 40 m. In the first case, there was a significantly greater abundance of locations of tortoises at the bottom of slopes (Table 4). In this case, the resulting ranking comes out as: bottom middle top; and: bottom > (middle + top).

At the small scale we found a similar pattern (Table 4), although fewer tortoises were detected at the top of slopes. The resulting ranking is: bottom middle top, and: (bottom + middle) > top.

Analyses for males and females did not show any differences in their abundance at either large or small scale.

DISCUSSION

ASPECT GRADIENT

In our study area, during the activity seasons (spring and autumn), spur-thighed tortoises were most abundant in north-westerly orientations at both local scales. To fully understand this pattern we should attempt to understand the differential habitat characteristics present in slopes of different aspects. Two key conditions/resources for the species - solar insolation and food - are expected to vary along this gradient as a result of microclimatic differences (Noy-Meir, 1973).

Solar radiation is highest on south facing slopes and lowest on north facing slopes. This radiation gradient leads to gradients in ground moisture and vegetation in the south-east of the Iberian peninsula with maxima in NNE facing and minima in SSE facing mountain systems (Ferrer Castán, 1994). This lack of complete coincidence between the solar and the moisture/vegetation gradients is due to the greater dryness of western orientations (evening insolation) as opposed to eastern orientations (morning insolation) (Dargie, 1984, 1987). With regard to food resources, *T. g. graeca* is a generalist herbivore that mainly feeds on herbaceous plants. In the other Iberian populations of the species, analyses of faecal pellets revealed 88 plant species belonging to 26 families (Andreu *et al.*, 2000). Annual

grass cover could be thus useful as an approximate descriptor of food availability. In that sense, the analysis of previous habitat data from the reserve (Anadón, 2002) showed that grass cover in the study area was greatest in the north-west, closely followed by the west, north and north-east, whereas minimum values were found in the south and south-east.

Thus, slopes where tortoises were more abundant (north-west facing) are assumed to have low-to-medium radiation rates and moderate to high levels of food resources. However, not all areas with high levels of food resources had equal tortoise abundance values. North-east facing slopes were rejected despite their abundance of annual grasses. It may be that these slopes, which have the shadiest aspect (Ferrer Castán, 1994), were too humid and cold for the species. In this case, thermoregulation could be the most important factor influencing abundance and habitat-use, and could even condition food-finding strategies. This agrees with the general patterns of habitat selection in ectotherms in temperate climates (Grant, 1990; Reinert, 1993). On the other hand, low abundance values of tortoises on south-facing slopes could be due to both lack of food resources, since these aspects presents the lowest values of annual grass cover, and thermoregulation. Thermoregulatory behaviour of *T. g. graeca*, as in most ectotherms in temperate climates, relies on a balance between the warming and cooling of their bodies, by both basking in the sun and resting in shadier and cooler areas (Lambert, 1981; Meek & Jayes, 1982; Sturbaum, 1982). South-facing slopes could be too hot for the species and may lack a proper combination of sunny and cool areas. Anyway, further field work and experimental studies are needed to fully address the thermoregulatory requirements of the species in relation to radiation rates and vegetation cover, and the specific distribution of food resources.

Aspect may give rise to areas with different habitat quality for the species and different tortoise densities, yielding an aggregated distribution pattern at a local scale. These results agree with those found by Andersen *et al.* (2000) on *Gopherus agassizii* in a location in the Mojave desert in which the variable that best explained habitat suitability for the species (defined in terms of the abundance of tortoises) was aspect. In relation to scale, the same abundance patterns related to aspect have emerged on the two scales we have employed. It suggests on one hand that the processes operating on these two scales are likely to be the same (Wiens, 1989) and, on the other, that the two scales may be useful in order to detect local abundance patterns.

Finally, it should be pointed out that the detected abundance pattern related to aspect is specific for the study area and it is expected to vary throughout the distribution range of the species wherever there is a climate gradient conditioning thermoregulatory strategies and the distribution of food resources. Moreover, under the same climatic conditions, differences in relief structure, usually associated with different lithologies, or different

successional stages in the vegetation, may lead to different landscape patterns and, thus, to different selection strategies and spatial patterns of abundance (Turner, 1989).

RUNOFF GRADIENT

Tortoises were most abundant in flat areas located in valley bottoms. Valley bottoms, mostly occupied by small non-irrigated crops, could be used for egg-laying, as has been observed in other *Testudo* populations (Swingland & Stubbs, 1985). On the other hand, crops in valley bottoms have a very high perimeter-area ratio (see Figs 1 and 2) and could be considered as edge-habitats between crops and shrubs. In this sense, edges have been identified as a favourite habitat in other reptiles (Blouin-Demers & Weatherhead, 2001, 2002).

The high frequency of tortoise locations in crops agrees with the positive effect at a local scale of open areas derived from human activities, as has been found in other species of tortoises in temperate regions (Auffenberg & Franz, 1982; Diemer, 1986; Kazmaier *et al.*, 2001). The use of crops by tortoises points towards future directions in research into the relation between the effects of traditional anthropic fragmentation and the use of edges by these species, a line of investigation that may provide useful insights into a number of conservation issues.

ACKNOWLEDGEMENTS

The authors would thank to Jose Antonio Palazón for helping with the GIS. José Antonio Sánchez-Zapata made very valuable comments on various stages of this work, improving both the form and content of the manuscript. Foundation 2001-Global Nature allowed us to work in its reserve. GRASS GIS is a free software under GNU; thanks to all those who have worked on its development. We would also like to give our heartfelt thanks to all those who took part in the field work.

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