Factors determining the distribution of the spur-thighed tortoise *Testudo graeca* in south-east Spain: a hierarchical approach

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This work represents the first attempt to model the habitat-species relationships of a species of terrestrial tortoise on a large scale. We applied hierarchical variance partition methodology to Generalised Lineal Models (GLMs), with the presence of the tortoise in 1 km² cells as the response variable. We posited the existence of a hierarchical scheme of factors (including climate, relief and lithology, and land-use) that determine the distribution of *Testugo graeca* in southeastern Spain. We also identified the environmental variables within each factor with the greatest explanatory power and decoupled local vs landscape effects. Climate, followed by relief and lithology, and then land-use, turned out to be the most important factor shaping the distribution of *T. graeca* in south-east Spain as well as determining the presence of the species within its range. Univariate models showed that the main climate constraints were related to rainfall and extreme minimum temperatures, two factors which could be related to constraints imposed by the length of the annual activity period and productivity. Finally, multi-scale decomposition suggested that neighbouring habitat and local dynamics may also be important in the distribution of the species at the landscape scale.

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Climate has been proposed as a key factor in the distribution and abundance of ectotherms (Kaspari and Valone 2002): temperature and rainfall co-limit primary production, thus limiting energy availability (Rosenzweig 1968), while solar radiation, measured as temperature, physiologically limits access to that production (Andrewartha and Birch 1954, Kaspari et al. 2000). The importance of these two limiting factors has been well corroborated in reptiles, especially in lizards (Dunham 1978, Congdon 1989, Grant and Dunham 1990, Adolph and Porter 1993, Sinervo and Adolph 1994). When compared to climate, other environmental factors such as relief, lithology, and land-use seem to be of secondary importance in the distribution of reptiles and merely act as modifiers of the habitat quality imposed by climate (Andersen et al. 2000, Guisan and Hofer 2003).

The spur-thighed tortoise *Testudo graeca* is a terrestrial tortoise with a western circum-Mediterranean distribution whose populations are severely threatened by habitat fragmentation and loss (Anon. 2004). Modelling species-habitat relationships at large scales has become very popular over the last decade and examples in ecology and conservation include many different types of taxa (Scott et al. 2002). Examples using terrestrial tortoises are, however, very scarce (but see Andersen et al. 2000 for a local scale). As ectotherms, terrestrial tortoises are likely to react strongly to environmental and, above all, climatic factors (Andrewartha and Birch

1954, Rosenzweig 1968, McKenney et al. 1998, Kaspari and Valone 2002). Furthermore, from an applied point of view, nearly all species of terrestrial tortoises are threatened (Klemens 2000) and their ranges usually are poorly known. Due to the difficulties in detecting the presence of tortoises, modelling seems to be the most efficient way of discovering the factors that determine tortoise distribution and abundance and of achieving accurate predictive distribution maps.

The general aim of this work was to study the environmental factors that determine the distribution of *Testudo graeca* at different spatial scales. Our first objective was to assess the differential importance of climate, relief and lithology, and land-use. We posited two hypotheses: 1) among these environmental factors, climate should be the most important, followed by relief and lithology and then by land-use; and 2) that this differential response may be organised hierarchically, with the most important factors acting mainly on larger scales. Our second objective was to assess the importance of individual variables within each of the environmental factors (climate, relief and lithology, and land-use) in order to identify any potential single ecological process shaping the distribution of the tortoise. Finally, our third objective was to decouple the response to the local vs landscape habitat features in relation to relief, lithology, and land uses. This point is of great interest since it may shed light on the importance of population processes in the distribution of this tortoise and provide insights in relation to habitat fragmentation that are relevant to the conservation of the species (Saab 1999, Sánchez-Zapata and Calvo 1999, Seoane et al. 2004).

Methods

Study area

We modelled the species-habitat relationships of *T. graeca* in the Region of Murcia (regional level) and within the species range (range level). The Region of Murcia is located in the southeastern Iberian Peninsula and covers an area of 11 317 km². Its climate is semi-arid Mediterranean with annual rainfall ranging from 200 to 570 mm. As species range we employed the limits described by Giménez et al. (2004). This distribution map locates the species in the southeast corner of the Region of Murcia with an area of 3060 km², equivalent to ca 60% of the species' total range in southeastern Spain.

Data of presence/absence of tortoises

Obtaining data on the presence/absence of terrestrial tortoises is a difficult task due to their low detectability. In the present work, the majority of the presence/absence data was collected from interviews with shepherds. Over many years shepherds work the same area daily and are thus a source of information of great quality about the absence or presence of the species. Only with sampling intensities as great as those made by shepherds is it possible to detect species at low densities or to assess reliable absences. We interviewed 132 shepherds in the southern of Region of Murcia in an area that largely contains the range of the species. Information derived from the interviews was incorporated onto a GIS system (GRASS GIS 5.0; <http://grass.itc.it/>) using a grid cell of 1 ×1 km. Interviews yielded 363 cells with information regarding the presence or absence of the species. For modelling purposes we also included data for northern Murcia, where the species is known to be absent; here, we randomly selected 456 cells that were automatically treated as absences. Similarly, we treated as presences those cells where the species is known to be present due to data from the authors or naturalists. In total we obtained information for 867 cells, including 235 presences and 632 absences.

Environmental characterisation

Cells with information regarding tortoise presence/absence were characterised with variables relating to climate, relief, lithology, and land-use (Table 1). Climatic variables were obtained from a climatic model constructed with historical series of data from 103 climate stations belonging to the Servicio Nacional de Meteorología in Murcia. Relief variables were derived from a Digital Terrain Model (resolution = 200 m). For lithological variables we employed maps published by the Inst. Español Geominero (1:50 000 scale). Variables related to land-use were obtained from the land-use map (1:50 000 scale) published by the Ministerio Español de Agricultura, Pesca, y Alimentación.

For continuous variables (those referring to climate, altitude, and slope), the value of each variable for the 1 ×1 km cells was taken as the mean value. For categorical variables (those referring to lithology, land-use, and aspect) the value of each 1 ×1 km cell was the dominant type. For relief, lithology, and land-use factors, as well as categorical variables on a 1 ×1 km scale ("1 ×1 variables"), we constructed another set of variables relating to the landscape composition around the cell. In these variables ("3 ×3 variables"), the value for each 1 ×1 km cell varied between 0 (variable not present in the cell nor in the eight surrounding cells) and 9 (variable dominant in the cell and in the eight neighbouring cells).

Table 1. Single environmental variables employed in the analyses. Climate variables area referred to a 1×1 km cell. Relief, lithology and landuses variables were constructed for 1×1 km and 3×3 km cells (see Methods for further details).

Climate	
R_{AN}, R_{SP}, R_{SU}, R_{AU}, R_{WI}	Annual, spring, summer, autumn and winter rainfall
T_{AN}, T_{SP}, T_{SU}, T_{AU}, T_{WI}	Annual, spring, summer, autumn and winter mean temperature
DEF_{AN}, DEF_{SP}, DEF_{SU}, DEF_{AU}, DEF_{WI}	Annual, spring, summer, autumn and winter mean water deficit values
ETP_{AN}, ETP_{SP}, ETP_{SU}, ETP_{AU}, ETP_{WI}	Annual, spring, summer, autumn and winter mean evapotranspiration values
TMIN	Mean of the minimum temperatures of the coldest month
FROST	Annual number of days that freezes
MINAVE	Annual mean of the daily minimum temperatures
Relief and lithology	
ALT	Altitude
SLO	Slope
SUN	Sunny aspect
SHD	Shady aspect
FLAT	Flat relief
CALC	Calcareous materials
SIL	Silicious materils
FSED	Fine texture sediments (loams, clays and sands)
CSED	Coarse texture sediments (conglomerate materials)
QUAT	Quaternary materials
VOLC	Volcanic materials
Land uses	
WOOD	Woodlands
SHRUB	Shrubland
DRYTREE	Dry tree crops
DRYHER	Dry herbaceous crops
IRTREE	Irrigated tree crops
IRHER	Irrigated herbaceous crops
IMP	Iimproductive land uses (urban, industrial)

Statistical procedures

All analyses were conducted both for the Region of Murcia and across the species' range. The importance of the different environmental factors (climate, relief and lithology, and land-use) was assessed by means of variance partitioning (Bocard et al. 1992). Variance partitioning has been employed by using direct gradient analysis (Bocard et al. 1992, Cushman and McGarigal 2002, Heikkinen et al. 2004). Here, we have adapted the variance partitioning method to multivariate Generalised Lineal Models (GLMs; McCullagh and Nelder 1989). Variance partitioning was also applied in a multilevel fashion (hierarchical variance partitioning; Cushman and McGarigal 2002) to analyse the role of local and landscape scales within the relief, lithology, and land-use factors.

A conceptual model of the hierarchical variance partitioning is represented in Fig. 1. The first tier of the decomposition separates the pure and joint effects of climate, relief and land-use on the distribution of the tortoise. In the second tier the variance explained by relief and lithology and land-use was separated into the pure and joint effects of the variables considered at

Fig. 1. Results of the variance partitioning for the distribution of *T. graeca*. Circles correspond to the total species variance accounted for by each individual variable subset. The three central circles represent the first tier partition whereas the two lateral pairs of circles represent the second tier partition. Two values are given for each component: the first left referred to the regional scale and the second right referred to inside the species' range.
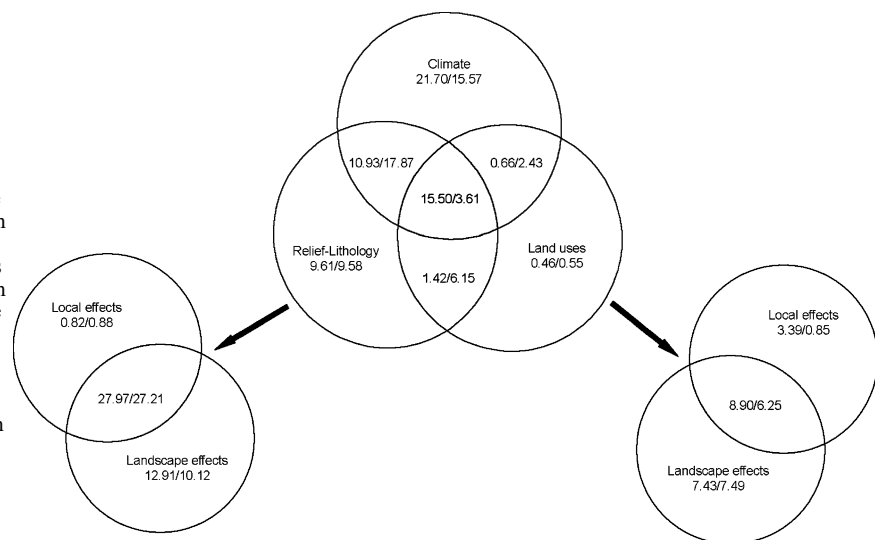
Table 2. Multivariate models for the presence of *T. graeca* within the Region of Murcia and within the species' range. R = % of explained variance.

	Model	R
Regional level		
Climate	$R_{AN}^2 + FROST^2 + ETP_{WI}^2$	53.43
Relief and lithology	$SIL3 \times 3 + ALT^2 +$ $QUAT3 \times 3 + SUN3 \times 3$	40.82
Land uses	$SHR3 \times 3 + DRYTREE3 \times 3$	17.89
Species' range level		
Climate	$FROST^2 + R_{WI}^2 + R_{SU} +$ $MINAVE + DEF_{SP} + ETP_{SU}$	39.43
Relief and lithology	$FSED3 \times 3 + ALT +$ $FLAT3 \times 3 + SIL3 \times 3 +$ $SHD3 \times 3$	35.37
Land uses	$SHURB3 \times 3 + WOOD3 \times$ $3 + DRYTREE3 \times 3$	13.74

landscape (3×3 variables) and local (1×1 variables) scales. In the case of the first tier, we first constructed multivariate models for each of the three factors (climate, relief and lithology, and land-use) using the presence/absence of tortoises as a response variable. The inclusion of variables into the models was made step-by-step using Akaike's information criterion (AIC; Burnham and Anderson 2002) as a selection criteria. Variables were added if they resulted in a $>1\%$ increase of the explained variance. Secondly, we extracted the variance explained by each of these models when considering the other models (or a combination thereof) as a co-variable set. Thirdly, we calculated the variance explained by each component in the first tier using basic algebra as per Anderson and Gribble (1998) and Cushman and McGarigal (2002). The calculation of the second tier partition was analogous to the first tier. To analyse separately the role of each of the environmental variables in the distribution of the tortoise, we constructed univariate GLMs. In order to account for the spatial autocorrelation of the data we included (in both univariate and multivariate models) a set of nine co-variables related to the spatial coordinates (x, y) of the locations: x, y, x^2, y^2, x^3, y^3, xy, x^2y and xy^2 (trend surface analysis, Legendre 1990, Legendre and Legendre 1998). Prior to this analysis, x and y were centred on their respective means to reduce co-linearity with higher order terms (Legendre and Legendre 1998). All analyses were conducted using the R statistical package (<http:// www.r-project.com/ >).

Results

Trend surface analysis explained 71.94 and 55.82%, respectively, of the variation in data on a regional scale and within the species' distribution range. When including the trend surface as a covariable set, no environmental variable or multivariate model yielded an

explained variance $>2.5\%$. Thus, in all the analyses we worked without the autocorrelation covariable set.

Importance of the different environmental factors

At the regional level, the total variance explained by all factors was 66.0%. Climate was the variable with the greatest pure and overall (pure+joints) effects (21.7 and 53.4%, respectively), followed by relief (9.6 and 41.2%, respectively; Table 2 and Fig. 1). Land-use explained 19.0% of the variance, although its pure effect was nearly null (0.5%). Regarding the joint effects, the effect of climate and relief individually with land-use were very small (2.6 and 2.5%, respectively), whereas the joint effect of climate and relief was much greater (15.7%). Finally, the amount of explained variance assigned to the three factors was also large (13.4%). Within the species' range, the total explained deviance was 55.8%. The ranking of the factors was the same as at regional level, although their relative importance, measured as their pure and joint effects, varied. In general, the explanatory power of climate and relief was lower and more similar at the regional level. The joint effect of the three factors was much smaller.

Landscape effects

For both the regional level and within the species' range, and for both relief and lithology and land-use factors, variables considered at local scale (1×1 km variables) presented very little explanatory power on their own, whereas the amount of variance explained by variables considered at the landscape scale on their own (pure effects) ranged from 26 to 51% of the total explanatory power of the factor (Fig. 1). Finally, the amount of variance assigned to the joint effect of the local (1×1 km) and landscape (3×3 km) variables was also large (between 43 and 72%, respectively, of the total of the factor).

Response to single environmental variables

At a regional scale, all climatic variables yielded significant models, most with a quadratic response (Table 3). Variables relating to rainfall presented the largest explained variance values (autumn rainfall $R^2 = 36\%$). *Testudo graeca* presented an optimum at ca 275 mm of annual rainfall (Fig. 1). Those variables relating to temperature presented the poorest models ($R^2 < 10\%$). Within the species' range, the explanatory power of climatic variables was notably less than at regional scale; only the quadratic response to the number of days with freezing temperatures ($R^2 = 9.97\%$) and a negative linear response to winter rainfall warranted consideration. The

Table 3. Respose of *T. graeca* to climate variables in the Region of Murcia and within the species' range. R =% of explained variance; type: type of response with the larger value of explained variance: "+": linear positive, "−" =linear negative; "++" = quadratic positive, "− −" =quadratic negative. n.s. =non significative response p >0.05.

variable	Regional level		Species' range level	
	R	type	R	type
RAN	26.51	++	n.s.	
RSU	22.28	++	n.s.	
RWI	9.06	−	6.49	−
RAU	36.39	++	2.25	++
RSP	18.21	++	2.54	+
TAN	7.15	++	2.34	−
TWI	8.76	++	3.56	−
TAU	7.37	++	3.38	−
TSP	7.68	++	2.51	− −
TSU	7.11	++	n.s.	
ETPAN	9.82	++	1.95	− −
ETPWI	12.14	++	5.80	−
ETPAU	8.20	++	1.23	− −
ETPSP	12.24	++	1.26	−
ETPSU	14.49	++	n.s.	
DEFAN	12.09	++	n.s.	
DEFWI	12.14	++	5.80	−
DEFAU	17.09	++	n.s.	
DEFSP	12.22	++	2.25	−
DEFSU	15.10	++	1.26	− −
TMIN	8.45	++	3.89	− −
MINAVE	6.14	++	3.15	−
FROST	10.66	++	9.97	++

variables relating to relief that yielded the most explanatory models at both levels were altitude, relief, and slope when considered at landscape scale (Table 4). Tortoises showed a strong positive response to siliceous lithology, with a quadratic response at 3×3 km and a positive linear response at 1×1 km, both in Murcia Province ($R^2 =33.91\%$, $R^2 =22.95\%$) and across the species' range ($R^2 =17.88\%$, $R^2 =12.53\%$). The strong negative response to limestone and calcareous strata within the species' range also is worth highlighting.

Among land-use variables, the proportion of shrubland at the landscape scale had the best adjustment (Table 5). Inside the species' range, maximum probability of presence of the tortoise was reached with ca 75% of shrubland cover in the nine 1 km^2 neighbouring cells (Fig. 2). The species showed a quadratic response to natural and extensive agricultural land-use in Murcia, although these responses were linearly negative when considered within the distribution range of the species.

Table 4. Respose of *T. graeca* to relief and lithology variables in the Region of Murcia and within the species' range. Variables with a percentage of explained variance R <1% are not shown. Type =type of response with the larger value of explained variance: "+": linear positive, "−" =linear negative; "++" =quadratic positive, "− −" =quadratic negative. n.s. =non significative response p >0.05.

variable	Regional level		Species' range level	
	R	type	R	type
ALT1 ×1	8.30	++	13.94	+
ALT3 ×3	7.59	++	14.22	+
SLO1 ×1	4.70	++	6.03	++
SLO3 ×3	10.86	++	15.53	++
SHD1 ×1	2.17	+	1.18	+
SHD3 ×3	4.06	++	3.81	++
SUN1 ×1	n.s.		1.91	+
SUNA3 ×3	3.41	++	4.90	++
FLAT1 ×1	3.49	−	4.62	−
FLAT3 ×3	9.69	++	14.73	++
CALC1 ×1	1.24	−	n.s.	
CALC3 ×3	1.76	−	n.s.	
SIL1 ×1	22.65	+	12.53	+
SIL3 ×3	33.91	++	17.88	++
CSED3 ×3	2.51	−	n.s.	
FSED3 ×3	9.14	−	20.83	−
QUAT1 ×1	5.70	−	15.14	−
VOL3 ×3	2.13	++	n.s.	

Table 5. Respose of *T. graeca* to relief and lithology variables in the Region of Murcia and inside the species' range. Variables with a percentage of explained variance R <1% are not shown. Type =type of response with the larger value of explained variance: "+": linear positive, "−" =linear negative; "++" =quadratic positive, "−−" =quadratic negative. n.s. =non significative response p >0.05).

	Regional level		Species' range level	
variable	R	type	R	type
WOOD	2.11	−	n.s.	
WOOD3×3	6.01	++	2.36	+
SHR	7.90	+	5.02	+
SHR3×3	13.10	++	9.74	++
DRYTREE1×1	n.s.		1.31	−
DRYTREE3×3	2.25	++	7.81	−
DRYHER3×3	4.40	++	1.93	−
DRYHER3×3	1.09	−	n.s.	
IRRHER1×1	n.s.		3.85	−
IRRHER3×3	1.63	++	5.25	−

Discussion

To our knowledge, this is the first work to have attempted to model the species-habitat relationships of a terrestrial tortoise on a large scale. The distribution of *T. graeca* responded strongly to environmental factors at both the regional scale and within its distribution range, as shown by the high values of total explained variance. As hypothesized, climate was the main factor shaping the distribution of *T. graeca* in southeast Spain and determining the presence of the species within its range, followed by relief and lithology and, lastly, land-use. Within the species' range, the differences between climate and relief and lithology were less whereas the role of land-use was greater. These patterns emerged sharply when considering the overall (pure plus joint) effects, although were not so clear when considering just the pure effect.

Methodologically, two issues should be noted. On one hand, the adaptation of the hierarchical variance partition methodology (Bocard et al. 1992, Cushman and McGarigal 2002) to Generalized Linear Models seems to have been successful. This fact is significant since GLMs are one of the most widely used tools in the analysis of species-habitat relationships (Guisan and Zimmermann 2000). On the other, trend surface analysis (Legendre 1990) failed to account for broadscale spatial trends and to analyse the effect of the environmental variables and factors at once. It is likely that this incapacity is related to the clumped distribution of the species at the two scales we have worked. As noted previously, trend surface analysis depends largely on the spatial distribution of the response variable (Lennon 2000).

Response to single environmental factors

Testudo graeca showed the strongest response to rainfall variables. Minimum extreme temperatures seem also to play an important role, since this factor was placed second in the multivariate analysis. Related to the maximum probability of presence of *T. graeca* around 275 mm of rainfall (Fig. 2), woodlands in Murcia begin to form continuous stands at above 300 mm of annual rainfall (Chaparro 1996). It is likely that above this rainfall value, the tree canopy, as it get closer, will hinder thermoregulation, thereby decreasing the potential activity periods of the tortoise and constraining the available time for energy acquisition. On the other hand, the low probability of presence below 275 mm may be related to poorer primary production and consequently low availability of food resource for this herbivorous tortoise. In relation to the annual number of frosts (Fig. 2), extreme minimum temperatures have been suggested as a key factor explaining the distribution of
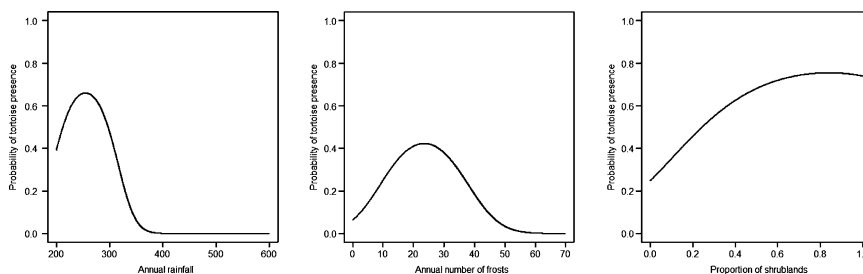

Fig. 2. Probability of presence of *T. graeca* in the Region of Murcia in relation to annual rainfall (left) and to annual number of frosts (center) and probability of presence of *T. graeca* inside the species' range in relation to the proportion of shrublands at the landscape scale (see methodology section for a further explanation of the variable) (right).

tortoises and turtles (St Clair and Gregory 1990, Morafka and Berry 2002). However, their relation with direct physiological constraints is debatable (Root 1988, 1989, Repasky 1991, Spicer and Gaston 1999, Gaston 2003). In our opinion, the upper distribution limit of frosts might be linked, as rainfall, with the length of annual activity periods. The spur-thighed tortoise is mainly active in spring (Pérez et al. 2002); in Mediterranean climate, areas with large number of frosts may be related to long winters and short springs and thus to short annual activity periods (Willemsem and Hailey 1999).

The effect of climate could be thus different at the two environmental extremes of the species' range, being likely to affect the length of the annual activity period at the northern limit of the species' range, and to affect the available energy within the system at the southern limit. These limiting processes agree with the general limiting processes expected in ectotherms (Andrewartha and Birch 1954, Rosenzweig 1968, Kaspari and Valone 2002) and coincide with those documented in other reptiles in altitudinal gradients at smaller spatial scales (Grant and Dunham 1990).

Within the species' range, *T. graeca* had a preference for mid-mountain areas and siliceous materials whereas flat reliefs and loamy and quaternary materials were strongly rejected. Lithology may play an important role in egg-lying and burrowing in tortoises (Morafka and Berry 2002). Siliceous materials are easily excavated, unlike loamy and quaternary materials that usually are highly compacted, especially when dried. These characteristics could hamper both egg-laying and the emergence of hatchlings. Similarly, *T. graeca* uses burrows to aestivate in summer (unpubl.) and they may be difficult to excavate or find in these lithologies. Regarding landuse, as expected, the tortoise prefered shrublands, whereas all agricultural uses were rejected.

Landscape effects

The strong response of the species to variables at the landscape scale (3 × 3 km) as compared to variables on a local scale (1 × 1 km) indicates that the presence of the species is dependent largely on characteristics of the neighbouring habitat at a larger scale than that of the individual (Saab 1999, Sánchez-Zapata and Calvo 1999).

The response of *T. graeca* to shrublands at a landscape scale (9 km^2) has interesting implications for conservation (Fig. 2). On one hand, up to 75% of shrubland cover, there is a positive relationship between the presence of the tortoise and shrubland cover, which indicates the importance of patch size for the survival of the species. Recent work based on population viability analysis has suggested that fragmentation processes are not a relevant factor in the conservation of *T. graeca* in

Greece and that any patch habitat, regardless of its size, is likely to support long-term viable populations (Hailey and Willemsem 2003). Our results suggest, however, that extinction dynamics associated with habitat fragmentation processes are likely to occur, at least in patch sizes of ca 1 km^2. On the other hand, above the threshold value of 75% of shrubland cover at the landscape scale, fragmentation processes seem to diminish and the probability of presence of *T. graeca* remained constant. This indicates that the species is linked to heterogeneous cultural landscapes, with a shrubland matrix where other uses (mainly non- irrigated crops) can also be included. These results agree with recent local studies carried out with radio-tracked individuals (Anadón et al. in press).

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