

Habitat selection by the spur-thighed tortoise *Testudo graeca* in a multisuccessional landscape: implications for habitat management

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Abstract. As a result of human activities, natural Mediterranean landscapes (including agro-ecosystems) are characterised by a mosaic-like structure with habitat-patches at different successional stages. These systems have high biodiversity levels and are home to a large number of species protected by European laws whose habitats should be adequately managed. In the present work, we study habitat use from an applied point of view in the spur-thighed tortoise *Testudo graeca*, an endangered reptile present in semi-arid Mediterranean agro-ecosystems. Results show that, at a landscape scale, the species selects simplified vegetation structures and includes in its home range re-colonisation shrubland and small non-irrigated fields. Within the home range, habitat selection patterns vary and areas with higher vegetation cover and complexity are selected. Detected patterns are discussed in terms of the ecological requirements of the species and with a hierarchical view of resources and conditions. The implications of our findings for habitat management aimed at the conservation of the species are also discussed.

Introduction

Historically, European ecosystems have been disturbed by human activity. This fact is especially relevant in the Mediterranean basin, where fires of anthropic origin, wood-extraction, grazing and low-intensity farming have all acted upon ecosystems dating from the Pleistocene (Le Honerou 1981). This human influence has led to the existence of semi-natural habitats or agro-ecosystems in which landscapes are characterised by a mosaic-like structure with habitat-patches at different successional stages reflecting the particular land-use history. These landscapes, also called cultural landscapes, have begun to disappear alarmingly over the last few decades owing to socio-economic changes in Mediterranean European countries. This decline has been speeded up recently by the Common Agricultural Policy (CAP), which has encouraged intensive farming in the most productive areas and the abandonment of large areas of marginal farmland (Baldock et al. 1996).

Cultural landscapes, characterised by intermediate levels of disturbance, are home to a great biodiversity (Bignal and McCracken 1996). A large number of species from these systems are included in the European Habitat Directive and many agro-ecosystems have been declared part of the Natura 2000 sites network. The question as to how exactly to manage these protected areas is nowadays one of the most important challenges facing environmental decision-makers in Europe (Oestermann 1998).

In the present work, we discuss management strategies for the conservation of the spur-thighed tortoise *Testudo graeca*, a threatened species living in multi-successional Mediterranean systems. Its main European population is located in southeast Spain in an area of 3000 km² (Giménez et al. 2001). The species is in serious decline throughout its range owing to habitat loss and fragmentation and its popularity as a pet (IUCN 2003). In southeast Spain the capture of the species for commercial purposes seems to have diminished in recent decades (Pérez et al. 2004). Thus, the main threat to the species is habitat loss and fragmentation caused mainly by the implantation of new irrigated farming schemes and the growth of towns and tourism (Giménez et al. 2001).

The species is classified as 'of interest' in the Habitats Directive and 11 Natura 2000 sites, with a total area of 800 km², have been declared to protect it. Apart from a number of other horizontal measures, these sites are the main tool for biodiversity management in the area. In this respect, the spur-thighed tortoise may also play a key role as a flagship species (Caro and O'Doherty 1999) in the conservation of a large portion of semi-arid Mediterranean ecosystems in southeast Spain (Esteve and Calvo 2000).

Throughout the distribution range of the species in southeast Spain, the original shrub vegetation was mainly formed of *Chamaerops humilis*, *Rhamnus lycioides*, *Periploca angustifolia*, *Pistacia lentiscus* and *Quercus coccifera* (López 2000), along with small patches of *Pinus halepensis* and *Quercus ilex* woodland (Chaparro 1996). Due to secular human activities (wood extraction, grazing and setting of fires), this vegetation has often given way to a less complex mixed shrub habitat with species such as *Rosmarinus officinalis*, *Artemisia* spp., *Thymus* spp. and *Genista* spp. These natural areas have been historically mixed with ploughed agricultural land (mainly non-irrigated crops). The extent of non-irrigated croplands has fluctuated throughout time, being closely linked with economic and demographic cycles. It is known, however, that its maximum extent was reached during the middle of the last century, when a great part of the distribution area of the spur-thighed tortoise was transformed in agricultural land. Since then, farming activity has decreased notably in the region, leading to the colonisation of abandoned fields by shrub vegetation dominated by *Anthyllis cytisoides*. These secondary-growth shrublands have less cover and a more simplified structure than the shrublands mentioned above. The abandonment of farmland has been encouraged by Common Agricultural Policies especially in marginal mountainous and semi-mountainous areas (Esteve et al. 1993).

In this study, we used radio-tracking to investigate habitat use in the spur-thighed tortoise in a traditional semi-abandoned landscape containing the

main vegetation units present in the distribution area of the species. The objectives were: (i) to study the habitat selection patterns at two different scales (home range location within the landscape and microhabitat within the home range); (ii) to discuss habitat selection patterns in relation to the main requirements for the species, and (iii) to analyze the implications of the results of the study for habitat management as a part of the conservation strategy of the species.

Methods

Study area

The study was carried out in the Biological Reserve 'La Galera' (Sierra de la Carrasquilla, Murcia, Spain). The reserve has ca. 90 ha. It has a mean annual rainfall of 295 mm and mean annual temperature of 18–19 °C. The altitudinal range of the reserve is 515–655 m a.s.l. The relief of the reserve is characterised by a system of *ramblas* (gullies) separated by hillsides of moderate-to-steep slopes composed of metamorphic (schist) and calcareous materials. The landscape structure is composed of a mosaic of the three main vegetation units present throughout the distribution of the species (see Introduction): shrublands dominated by *Anthyllis cytisoides*, mixed shrublands (*Rosmarinus officinalis*, *Artemisia barrelieri*, *Helianthemum almeriense*) and small non-irrigated fields at the bottom of the *ramblas*. There are also patches of the perennial grass *Stipa tenacissima*. Typical species from the original mature shrublands, characterised by their larger size and cover (mainly *Rhamnus lycioides*), are scattered all over the study area, especially in the mixed shrublands. However, they do not form a distinguishable vegetation unit. According to regional habitat models, the reserve contains optimum habitat for the species in relation to climate, relief and lithology (Giménez et al. 2001). On the basis of capture–recapture studies, mean density values of tortoises in the reserve is around 17 ind/ha (authors, unpublished data).

Animal biometry and tracking

During 1 year (from June to June) we radiotracked 10 adult tortoises (six females and four males). Transmitters (AYAMA TRS2, SEGUTEL, Barcelona, Spain) were attached to the lateral-anterior part of the caparace with an epoxy glue. The weight of the transmitters (from 10 to 20 g) was less than 5% of the weight of the animals (White and Garrot 1990). We considered individuals over 7 years old to be adults (Andreu et al. 2000). Growth rings of the caparace scutes were used to estimate age (Castanet and Cheylan 1979; Germano and Bury 1998). Males and females were distinguished visually by secondary sexual characteristics (Andreu and López-Jurado 1998).

Individuals were located once per week, 2 weeks out of every 3 weeks, usually in the mid-day. Locations were recorded with a GPS (GeoExplorer 3.0, Trimble) with an error of 1–3 m.

Habitat characterisation

The study area was characterised by six variables concerning land-use history, vegetation structure and aspect. The land-use history variable had three classes: mixed shrubland (old shrublands), re-colonisation shrubland and cropland. The perimeter of cropland areas was geo-referenced in the field with a GPS (GeoExplorer 3.0, Trimble). For mapping mixed and re-colonisation shrubland we digitized and compared aerial photographs dating from 1999 (current situation) and 1955, when the amount of cropland was at its greatest. We considered those areas ploughed in 1955 but not in 1999 to be re-colonisation shrubs, whereas those areas not ploughed neither in 1955 nor in 1999 were considered to be mixed shrubs. In order to characterise the vegetation structure we made a systematic sampling of the vegetation. We used circular sample plots with a radius of 3m located every 20 m in the form of a grid (number of samples = 738). We also established non-systematic plots wherever there were sudden changes in vegetation cover. In every plot we measured four vegetation variables: shrub cover (>25 cm height, generally including species such as *A. cytisoides*, *R. officinalis*, *Helichrysum stoechas* or *Cistus* spp.), low shrub cover (<20 cm height with species such as *Thymus* spp., *Helianthemum almeriense* or *Artemisia* spp), *S. tenacissima* cover and annual grass cover. The perennial grass *S. tenacissima* was considered as a separate group since it forms monospecific patches with a different structure from other shrub species. For each variable we considered five cover classes: less than 10% cover, 11–33%, 33–50%, 51–66% and more than 67%. Cover was measured visually with a previous calibration among the samplers. With the help of a GIS (GRASS 5.0; GRASS Development Team 1999; <http://grass.itc.it/>) we constructed vegetation maps of the four variables using interpolation techniques.

Aspect was characterised by a Digital Land Model 1:5000. In order to map the different aspect patches we used first-, second- and third-order watersheds as references. Nine classes were considered: N, NE, E, SE, S, SW, W, NW and F (flat areas, usually in valley bottoms).

Habitat selection analysis

For the habitat selection analysis, we adopted a hierarchical approach of habitat selection at a local scale (Johnson 1980; Schaeffer and Messier 1995). According to this approach, there are different selection levels in both space and time. At each of these levels requirements may differ and thus lead to different selection patterns. The most commonly employed spatial levels, and the ones which we

have employed here too, are the location of the home range and selection within the home range (levels II and III of Johnson 1980). It has been proposed recently that this spatial hierarchy could be directly related to a hierarchy of conditions and resources. Habitat selection patterns should enable animals to avoid the negative effects of factors that mostly limit individual fitness, and should be strongest at the largest scales of selection. Less important limiting factors may influence selection patterns only at smaller scales (Rettie and Messier 2000).

We carried out our habitat selection analysis by means of a compositional analysis (Aebischer et al. 1993) based on a search for differences between available habitats and the habitats actually used by animals. The compositional analysis had three steps. First, we tested for the overall departure from random habitat use. If there was a habitat-use pattern that differed from a random pattern, the next step was to rank the habitats in order of use by comparing the pairwise differences between habitats. Finally, significant differences between pairs of habitats were assessed. We performed a compositional analysis at two scales or levels. At the first level, we compared the home range habitat composition vs. the total study area habitat composition. At the second level, we compared the proportion of habitats used as based on the ratio between radio-locations and home range habitat composition. These two levels have a different biological significance: the upper level indicates selection patterns on a landscape level, whereas the second level indicates the habitat or microhabitats that are actually occupied by the animal.

We performed a compositional analysis on these two levels for the six habitat variables, for all individuals and for females separately. Analysis for males separately were not performed due to its small sample size (Aebischer et al. 1993). For each habitat variable, classes were pooled when necessary for the compositional analysis and non-utilised but available habitats were replaced by 0.01%, following Aebischer et al. (1993). The definition of true availability is problematical since it is an arbitrary decision (Johnson 1980; Aebischer et al. 1993). Here, we have defined the study area as being all the slopes where animals were located, while the home range was estimated with the Minimum Convex Polygon (MCP; Mohr 1947). For the delimitation of the study area and the estimation of home range we used all locations (one location per week, 2 weeks out every 3 weeks) during 1 year. For habitat analysis we employed all locations, leaving out consecutive repeated locations that denoted inactivity (hibernation and aestivation). These periods of inactivity extended for over 6 months (Pérez et al. 2002) and their inclusion in the analysis would have led to a description skewed towards their annual refuges rather than the habitat actually used during activities such as feeding, thermoregulation, egg-laying and courtship.

Results

Total number of locations per individual, including consecutive repeated locations, varied between 30 and 35. The resulting study area for analysis

purposes had 31 ha (see Methods). Mean home range size using the MCP estimator was 1.71 ± 1.61 ha for all individuals. Mean home range size for males was 2.56 ± 3.02 ha for males and 1.15 ± 0.15 ha for females. A Wilcoxon test did not detect significant differences in the home range size between sexes ($p = 0.201$).

The number of locations employed for habitat analysis was lower. After excluding repeated locations, six tortoises had 24 different locations along the year, whereas four tortoises that presented a reduced (or even null) autumn activity period had from 14 to 21 activity locations.

Selection at landscape level

For all individuals, patterns of habitat selection were detected for all variables, except for low shrub cover and *S. tenacissima* cover (Table 1). Tortoises selected croplands in their home ranges, while the least selected vegetation unit was mixed shrublands. There was also a preference for areas with low cover values for shrubs. Tortoises selected areas with intermediate annual grass cover, rejecting areas with minimum and, above all, maximum values for annual grass cover. Regarding aspect, individuals located their home ranges on slopes facing west and northwest and flat areas, whereas areas facing east and northeast were very much avoided.

Separate analyses for females maintained the general pattern (Table 2).

Selection within the home range

Analyses for all individuals within the home range were only significant for two variables (Table 1). Tortoises rejected places with high cover values for shrubs and for *S. tenacissima*. However, analyses for females were significant for a large number of variables (Table 2). Females selected places with very low shrub cover, low shrubs and *S. tenacissima* cover, and did not show any habitat pattern related to annual grass cover. Places used by females were generally located on east- or northeast-facing slopes and flat areas were the least used. The land-use history did not yield any selection pattern. However, when we compared all shrub areas (re-colonisation shrubland and mixed shrubland) with croplands, females showed a preference for places with natural vegetation.

Discussion

Selection at landscape scale

Results showed that spur-thighed tortoises prefer re-colonisation shrubland and cropland over more complex mixed shrubland, which agrees with a selection for low vegetation cover values. Numerous studies on habitat selection by

Table 1. Results of the compositional analysis for all individuals and for the two levels of comparison.

All Individuals	Study area/home range		Home range/radiolocations	
	<i>p</i>	Ranking	<i>p</i>	Ranking
Land use	0.0036	Crops > > > Col. shrubs > Mixed shrubs	0.0530	n.s.
Annual grass cover	0.0008	2 > 3 > 1 > > > 4	0.1717	n.s.
<i>S. tenacissima</i> cover	0.0706	n.s.	0.0461	1 > 2 > > > 3-4-5
Shrub cover	0.0012	1 > > > 3 > 2 > 4 > 5	0.0115	4 > 3 > 1 > 2 > > > 5
Low shrub cover	0.1977	n.s.	0.4383	n.s.
Orientation	0.0229	NW > W > F > > > SW > S > > > SE > N > E > NE	0.6841 (A)	n.s.
			0.1579 (B)	

For each variable and for each level of comparison the significance level (*p*) and the resulting preference ranking is shown. 'n.s.' indicates non-significant ranking. '>' indicates greater use (but not significant), whereas '>' '>' '>' indicates significant difference in use between the two classes. Classes of cover: 1, < 10% cover; 2, 11–33%; 3, 34–50%; 4, 51–66%; 5, > 67% cover.

Table 2. Results of the compositional analysis for females and for the two levels of comparison.

Females	Study area/home range		Home range/radiolocations	
	<i>p</i>	Ranking	<i>p</i>	Ranking
Land use	0.0149	Crops > Col. shrubs > Mixed shrubs	0.0493	Shrubs* > Crops
Annual grass cover	0.0004	2 > 3 > 1 > > > 4	0.4096	n.s.
<i>S. tenacissima</i> cover	0.2645	n.s.	0.0414	1 > 2 > 3-4-5
Shrub cover	0.0021	1 > > > 3 > 5 > 4 > 2	0.0234	1 > > > 3 > 4 > 2 > 5
Low shrub cover	0.2851	n.s.	0.0055	1 > > > 2 > 3 > 4
Orientation A	0.0055	W-NW > S-SW > > > F > > > E-SE > N-NE	0.0531	n.s.
Orientation B	0.0023	NW-N > SW-W > > > F > > > SE-S > NE-E	0.0107	NE-E-SE-S > SW-W-NW-N > f

For each variable and for each level of comparison the significant level and the resulting preference ranking is shown. 'n.s.' indicates non-significant ranking. '>' indicates greater use, whereas '> > >' indicates significant difference in use between the two classes. Classes of cover: 1, < 10% cover; 2, 11-33%; 3, 34-50%; 4, 51-66%; 5, > 67% cover. Variables 'Orientation A' and 'Orientation B' result from the pooling of the classes of the former variable 'Orientation', made in order to address the requirements of the compositional analysis (Aebischer et al. 1993) (*) Variable 'shrubs' comprises both colonization and mixed shrubs.

ectotherms have confirmed the importance of habitat structure in thermoregulation (e.g. Litzgus and Brooks 2000; Bryant et al. 2002). The preference for areas with an open vegetation structure is likely to be linked to the thermoregulation requirements of tortoises. The preference of *T. graeca* for low cover values has also been indicated by other authors (Wright et al. 1988, Willemsem 1991). The strong selection for non-irrigated croplands could also be due to its role in egg-laying, as is the case in other *Testudo* populations (Stubbs and Swingland 1984; Swingland and Stubbs 1985). On the other hand, it has been shown that the ecotones between crops and natural vegetation areas are optimum places for thermoregulation in the black rat snake (Blouin-Demers and Weatherhead 2001a, b), because they contain basking places near shadier areas where animals can cool down.

The spur-thighed tortoise selects areas with intermediate annual grass cover and rejects areas with very high or very low cover. Annual grass cover could be useful as an approximate descriptor of food resource availability. Andreu et al. (2000) determined the presence of more than eighty plant species in the diet of *T. graeca*, corresponding to 21 genera, with a predominance of grasses and other annual herbaceous plants. The rejection of areas with the highest annual grass cover values suggests that conditions in these areas are not appropriate for the species and that grass cover preference is related to other factors than feeding resource availability. Highest values of annual grass cover are obtained in the coolest and shadiest areas facing north and east (Anadón 2002), areas which may have low thermal quality for tortoises.

Tortoises had a preference for northwest- and west-facing slopes, whereas those facing east, north and, above all, east, were clearly rejected. This pattern agrees with the results obtained from analysing census data (Anadón et al. in press). The selected range may be a reflection of a trade-off between thermoregulation and feeding requirements. North and northeast slopes are the shadiest, most moist and with the greatest vegetation cover areas (Ferrer Castán 1994), and may be the least preferred because they strongly restrict thermoregulation. On the other hand, southwest, south and southeast slopes, are the warmest and most arid orientations (Ferrer Castán 1994) and present the lowest values for annual grass and vegetation cover (Anadón 2002). These slopes could be rejected for both feeding and thermoregulation issues.

Our results suggest that in a multi-successional landscapes the requirements of *T. graeca* (mainly thermoregulation, feeding and egg-lying) may be better satisfied in the early stages of the successional gradient (colonisation by shrubs and small non-irrigated croplands). However, this selection process is constrained by environmental heterogeneity caused by relief factors (for example, low preference for more arid areas facing south and, especially, for more shady areas facing north–northeast). The role of open areas is likely to vary along the environmental gradient of the distribution area of *T. graeca*. For example, open areas are probably more valuable in the northern part of the range, where the vegetation cover is more closed, than in the southern part, where arid conditions naturally lead to more open shrublands.

Selection patterns inside the home range

Inside home ranges, there was a very weak overall response of all individuals. Females separately, however, showed more marked patterns. This suggests a differential habitat response between sexes. Females tended to select areas of natural vegetation (mixed and re-colonisation shrubs) compared to crops. It implies an inversion of the habitat selection patterns with scale: habitats that are selected at a landscape level are, however, not intensively used along the whole activity period. The ecological requirements that are behind the detected patterns (such as food resources, places for egg-lying or for thermoregulation purposes or shelter) may not be important within the home range considering the annual cycle, although they could be significant in particular periods of the year. Regarding this point, patterns detected at lower spatial scales are assumed to correspond to processes operating on smaller temporal scales (Rettie and Messier 2000; McLoughlin et al. 2002). The annual cycle seems an appropriate time scale in which to detect selection processes at a landscape scale (position of the home range), although this scale may be too coarse for analysis within the home range. Seasonal selection analysis could yield more precise information regarding the spatial location of requirements within the home range.

Implications for habitat management

Our results showed that spur-thighed tortoises selected habitat features found in the early stages of vegetation succession (croplands, re-colonisation shrubs). The maintenance of small-scale non-irrigated croplands may increase the habitat quality for the species, as has also been suggested for *T. hermanni* (Stubbs and Swingland 1984; Swingland and Stubbs 1985). However, regional habitat models (Giménez et al. 2001) have shown that large areas of non-irrigated cropland have a negative effect on the species and probably promote fragmentation processes. Therefore, the positive effect of non-irrigated croplands must be seen in the context of a landscape with a fine-grained mosaic structure.

The preference for intermediate successional stages has been noted in other species of tortoises (Auffenberg and Franz 1982; Stubbs 1995; Kazmaier et al. 2001). In the distribution area of *T. graeca* in southeast Spain, the generation and maintenance of intermediate vegetation stages has been historically related to relief, natural fires and the action of wild herbivores. Heterogeneous landscapes have been favoured by traditional forms of land-use and nowadays most intermediate successional stages of vegetation are of anthropic origin. These habitats are found today in cultural landscapes where shrubs are cut down and grazed, two activities which may have a positive effect on *T. graeca*. An important proportion of the range of the species in southeast Spain is composed of re-colonisation shrublands coming from abandoned croplands. The

abandonment of large areas of continuous croplands in the 1950s has probably had a positive, though ephemeral, effect on the species. It has been hypothesised that vegetational succession can have a significant impact upon habitat availability for ectotherms by affecting the thermal characteristics of habitats (Meik et al. 2002; Pringle et al. 2003). Furthermore, several studies have related local extinctions of reptile populations with successional vegetation changes (Ballinger and Watts 1995; Jäggi and Baur 1999). Classical conservation policies, based on non-intervention, may thus lead to a decrease in habitat quality due to an encroachment of shrublands within natural succession dynamics. Management measures that lead to an increase in vegetation cover, such as reforestation, may also have a negative effect on the species. This management consideration agrees with those made for other terrestrial tortoises (USFWS 1990; Diemer 1986; Montori et al. 2001).

Some semi-arid Mediterranean shrublands are protected under European directives and should be managed accordingly (CEE Habitat Directive 92/43). Habitat management in the areas inhabited by the spur-thighed tortoise should consist of a trade-off between direct tortoise management actions (to favour immature stages of vegetation) and vegetation management (that will lead to mature stages of vegetation). The maintenance of a fine-grained landscape mosaic with patches of different complexity (and land-uses) could conceal these two conservation strategies. This could be achieved by adequate agro-environment schemes (Kleijn and Sutherland 2003). In this sense, the latest reforms of the PAC (2078/1992; 1782/2003 EEC) have integrated measures for biodiversity conservation issues that could be useful (Ormerod et al. 2003). However, current policies are far from solving the problem of the conservation of semi-natural areas or agro-ecosystems (Oestermann 1998), and further efforts are needed.

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References

- Aebischer N.J., Robertson P.R. and Kenward R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.
- Anadón J.D. 2002. Uso del hábitat de la tortuga mora *Testudo graeca graeca* en el sureste ibérico. PhD minor thesis. Departamento de Ecología e Hidrología de la Universidad de Murcia, Murcia.

- Anadón J.D., Giménez A., Pérez I., Martínez M. and Esteve M.A. The role of relief in the local abundance patterns of the spur-thighed tortoise *Testudo graeca graeca*. Herpetol. J. In Press.
- Andreu A.C., Díaz-Paniagua C. and Keller C. 2000. La tortuga mora (*Testudo graeca* L.) en Doñana. Asociación Herpetológica Española. Monografías de Herpetología 5: 1–70.
- Andreu A.C. and López-Jurado L.F. 1998. Los reptiles ibéricos: género *Testudo*. In: Ramos Sánchez M.A. (ed.), Reptiles. CSIC, Madrid, pp. 109–124.
- Auffenberg W. and Franz R. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). In: Bury R.B. (ed.), North American Tortoises: Conservation and Ecology. USDI, USFWS. Wildlife Research Report 12: 95–126.
- Baldock D., Beaufoy G., Brouwer F. and Godeschalk F. 1996. Farming at the margins – abandonment or redeployment of agricultural land in Europe. Technical report IEEP. London and IBN-DLO, The Hague.
- Ballinger R.E. and Watts K.S. 1995. Path to extinction: impact of vegetational change on lizard populations on Arapaho Prairie in the Nebraska Sandhills. Am. Midland Nat. 134: 413–417.
- Bigal E.M. and McCracken D.I. 1996. Low intensity farming systems in the conservation of the country side. J. Appl. Ecol. 33: 423–424.
- Blouin-Demers G. and Weatherhead P.J. 2001a. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology 82(11): 3025–3043.
- Blouin-Demers G. and Weatherhead P.J. 2001b. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented landscapes. Ecology 82(10): 2882–2896.
- Bryant S.R., Thomas C.D. and Bale J.S. 2002. The influence of thermal ecology on the distribution of three *Nymphalid* butterflies. J. Appl. Ecol. 39: 43–55.
- Caro T.M. and O'Doherty G. 1999. On the use of surrogate species in conservation biology. Conserv. Biol. 13(4): 805–814.
- Castanet J. and 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: 1649–1665.
- Chaparro J. 1996. Distribución potencial del bosque y de sus especies arbóreas en zonas semiáridas: modelos y aplicaciones. Ph D Thesis Universidad de Murcia, Murcia.
- Diemer J.E. 1986. The ecology and management of the gopher tortoise in the southeastern united states. Herpetologica 42: 125–133.
- Esteve M.A., Calvo J.F., Ibernón M., Giménez A., Palazón J.A. and Ramírez-Díaz L. 1993. Tierras marginales en ecosistemas semiáridos del sureste ibérico: descriptores, relación con los factores físicos y aplicaciones a la gestión ambiental. In: Ortiz R. (ed.), Problemática Ambiental y Desarrollo. V Reunión Nacional de Geología Ambiental y Ordenación del Territorio, Murcia, pp. 777–786.
- Esteve M.A. and Calvo J.F. 2000. Conservación de la naturaleza y biodiversidad en la Región de Murcia. In: Calvo J.F., Esteve M.A. and López F. (Coord). Biodiversidad: Contribución a su conocimiento en la Región de Murcia. Servicio de publicaciones de la Universidad de Murcia, Murcia, pp. 193–214.
- Ferrer Castán D. 1994. Variaciones espaciales de la vegetación de la Sierra de Cartagena (Sureste Ibérico). El análisis de gradientes y los problemas de escala. PhD thesis. Universidad de Murcia, Murcia.
- Germano D.J. and Bury R.B. 1998. Age determination in turtles: evidence of annual deposition of scute rings. Chelonian Conserv. Biol. 3: 123–132.
- Giménez A., Esteve M.A., Anadón J.D., Martínez J., Martínez M. and Pérez I. 2001. Bases ecológicas para una estrategia de conservación de la tortuga mora en la Región de Murcia. Technical report. Consejería de Agricultura, Agua y Medio Ambiente de la Región de Murcia, Murcia.
- IUCN. 2003. 2003 IUCN Red List of Threatened Species. Gland, Switzerland.
- Jäggi C. and Baur B. 1999. Overgrowing forest as a possible cause for the local extinction of *Vipera aspis* in the northern Swiss Jura mountains. Amphibia-Reptilia 20: 25–34.

- Johnson D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- Kazmaier R.T., Hellgreen E.C. and Ruthven D.C. 2001. Habitat selection by Texas tortoise in managed thornscrub ecosystem. *J. Wildlife Manage.* 65(4): 653–660.
- Kleijn D. and Sutherland W.J. 2003. How effective are European agro-environment schemes in conserving and promoting biodiversity?. *J. Appl. Ecol.* 40: 947–969.
- Le Honerou H.N. 1981. Impact of man and his animals on Mediterranean vegetation. In: Di Castri F., Goodall D.W. and Spetch R.L. (eds), *Ecosystems of the World II, Mediterranean Shrublands*. Elsevier Scientific, Amsterdam.
- Litzgus J.D. and Brooks R.J. 2000. Habitat and temperature selection of *Clemmys guttata* in a northern population. *J. Herpetol.* 34: 178–185.
- López J.J. 2000. Respuesta ambiental de las principales especies arbustivas en sistemas áridos y semiáridos mediterráneos: modelos y aplicaciones. PhD thesis. Universidad de Murcia.
- Meik J., Jeo R., Mendelson J. and Kens K. 2002. Effects of bush encroachment on an assemblage of diurnal lizard species in Central Namibia. *Biol. Conserv.* 106: 29–36.
- McLoughlin P.D., Case R.L., Gau R.J., Cluff H.D., Mulders R. and Messier F. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132: 102–108.
- Mohr C.O. 1947. Table of equivalent populations of North American small mammals. *Am. Nat.* 37: 223–249.
- Montori A., Llorente G.A., Carretero M.A. and Santos X. 2001. La gestión forestal en relación con la herpetofauna. In: Camprodon J. and Plana E. (eds), *Conservación de la biodiversidad y gestión forestal. Su aplicación a la fauna vertebrada*. Edicions Universitat de Barcelona, Barcelona, pp. 251–290.
- Oestermann O.P. 1998. The need for management of nature conservation sites designated under Natura 2000. *J. Appl. Ecol.* 25: 968–973.
- Ormerod S.J., Marshall J.P., Kerby G. and Rushton S.P. 2003. Meeting the ecological challenges of agricultural change: editors' introduction. *J. Appl. Ecol.* 40: 939–946.
- Pérez I., Giménez A., Anadón J.D., Martínez M. and Esteve M.A. 2002. Patrones de actividad estacional y diaria de La tortuga mora *Testudo graeca graeca* en el sureste ibérico. *Anales de Biología* 24: 65–75.
- Pérez I., Giménez A., Sánchez-Zapata J.A., Anadón J.D., Martínez M. and Esteve M.A. 2004. Non-commercial collection of spur-thighed tortoises: a cultural problem in southeast Spain. *Biol. Conserv.* 118: 175–181.
- Pringle R.M., Webb J.K. and Shine R. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Holocephalus bungaroides*. *Ecology* 84(10): 2668–2679.
- Rettie W.J. and Messier F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23: 466–478.
- Schaefer J.A. and Messier F. 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18: 333–344.
- Stubbs D. 1995. *Testudo hermanni* in France. In: Ballasina D. (ed.), *Red Data Book on Mediterranean Chelonians*. Edagricole-Edizioni Agricole, Bologna, Italia, pp. 94–102.
- Stubbs D. and Swingland I.R. 1984. The ecology of a Mediterranean tortoise (*Testudo hermanni*): a declining population. *Can. J. Zool.* 63: 169–189.
- Swingland I.R. and Stubbs D. 1985. The ecology of a Mediterranean tortoise (*Testudo hermanni*): reproduction. *J. Zool. Lond. (A)* 205: 595–610.
- U.S. Fish and Wildlife Service. 1990. Gopher Tortoise Recovery Plan. U. S. Fish and Wildlife Service, Jackson, Mississippi.
- Willemsen R.E. 1991. Differences in thermoregulation between *Testudo hermanni* and *Testudo marginata* and their ecological significance. *Herpetol. J.* 1: 559–567.
- White G.C. and Garrot R.A. 1990. *Analysis of Wildlife Radio-tracking Data*. Academic Press, San Diego.
- Wright J., Steer E. and Hailey A. 1988. Habitat separation in tortoises and the consequences for thermoregulation and activity. *Can. J. Zool.* 66: 1537–1544.