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Specialist and generalist species in habitat use: implications for conservation assessment in snakes

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Abstract

Habitat specialization is recorded as one of the central factors that make species vulnerable to extinction. Among snakes, there is considerable variation in this trait, as some species are specialists and others are generalists in habitat use. We have quantified habitat specialization in the snakes of the southern Iberian Peninsula, and compared it with their abundance and IUCN categories. All data were combined for a principal components analysis that discriminated two main groups: three generalist species that live in all types of habitat, and five specialist species that ranged from rather scarce to extremely rare and are found only in unaltered habitats. The three generalist snakes are not threatened and their IUCN category is Least Concern. Three out of the five specialist species are categorized as Near Threatened, Vulnerable, and Endangered at regional or national levels. The other two species are currently considered Not Threatened and we discuss whether they are incorrectly classified. The conservation status of snakes is difficult to evaluate because of their secretive habits and low population densities. We suggest that quantifying habitat specialization may be a useful tool for assessing the conservation status of secretive organisms such as snakes.

Keywords: *Conservation, habitat use, Iberian Peninsula, IUCN categories, snake*

Introduction

The main threats to animal populations in the world are habitat destruction and fragmentation (Wilson 1992; Hilton-Taylor 2000). Human degradation of natural systems has caused a massive loss of biodiversity in developed and highly industrialized countries. Although literature on the effects of human activities on herpetofauna is scarce, habitat loss appears also to be the most serious threat to reptiles (Dodd 1987, 1993; Gibbons et al. 2000). Reptile species respond unequally to habitat alteration, as several ecological and biological factors make some of them more sensitive than others to habitat disturbance (Reed and Shine 2002; Santos et al. 2006, 2007a). Likewise, some species decline with

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anthropogenic changes in landscape, whereas others thrive and even increase in altered habitats (McLay 1974; Case 1996). Snakes usually have a low capability to respond to habitat alteration (Filippi and Luiselli 2000), although species which occupy a high diversity of habitats, “generalist species”, are expected to be globally less vulnerable to habitat disturbance than species restricted to a small number of habitats, “specialist species”. It appears that habitat specialization is an important factor in determining the vulnerability of the species, as snakes respond to altered habitats depending on their specialization in habitat use (Foufopoulos and Ives 1999; Reed and Shine 2002). In snakes, an approach to their conservation status through the analysis of habitat use is highly reliable because of the close correlation between habitat use and physiological condition in this group of ectotherms (Reinert 1993). The use and selection of optimum habitats improve performance and individual fitness (Huey 1991).

In regions with historical human-related disturbance of habitat, we can analyse whether generalist and specialist species in habitat use differ in their conservation status. This analysis seeks the possible existence of a differentiated response by species to habitat alteration. This relationship is here assessed in a snake community of the southern Iberian Peninsula, a Mediterranean region historically modified by humans (Blondel and Aronson 1999). Data on one dimension of the ecological niche such as the habitat are scarce for snakes, largely due to the secretive nature of these reptiles and the difficulty of observing them under natural conditions (Reinert 1993). Here, we combine data for many years of tracking snakes in order to describe habitat utilization by the snake community in the south-eastern Iberian Peninsula, hence describing the generalist and specialist snake species, and relating this distinction to the conservation status of each species in this region.

Material and methods

Study area

The study area is located in the south-eastern Iberian Peninsula, covering approximately 2,500,000 ha (2°30′–4°15′W, 36°45′–38°30′N). Because of its geographic position and altitudinal variability, this region is characterized by high habitat diversity. The study area has a Mediterranean climate with strong seasonality: hot, dry summers, and cold winters with frequent frosts. The average annual temperature varies from 4°C at the highest altitudes with snake populations (i.e. Sierra Nevada, 3000 m a.s.l.) to 18.5°C at the seashore, and the annual rainfall ranges from 1300 mm to less than 270 mm. This region has suffered historical pressures for land use changes and degradation, including intensive agriculture, pine afforestation, and urbanization, as major causes of habitat alteration (Rundel et al. 1998). These alterations have given rise to fragmentation of Mediterranean forest and scrub.

In the study area are found five out of the six categories of Mediterranean bioclimatic thermotypes (Rivas-Martínez 1987), established by the criteria of phytogeographic zonation of vegetation according to thermo-climatic parameters (mean annual temperature, mean minimum temperature of the coldest month, and mean maximum temperature of the coldest month) that change with altitude and/or latitude (Rivas-Martínez 1987). For the five thermotypes, several habitats are differentiated and defined as landscape units. A total of 25 habitats was defined, including natural vegetation types, stands of afforested pine, and cultivated as well as urbanized areas that accounted for the geometric configuration of the landscape in the study area (Table I). The surface area of each habitat

Table I. Habitat classification in the study area (southern Iberian Peninsula).

Bioclimatic thermotypes	Habitats	Alteration level	Surface area (ha)	Number of citations	Species richness
Thermo-Mediterranean (0–600/1000 m)	Sandy beach	3	60.7	4	3
	Grass land	3	24,013.4	13	4
	Shrub	2	105,532.8	23	4
	Gallery forest	2	4,240.8	4	2
	Pine stand	3	13,407.8	16	5
	Cereal crop	3	81,929.6	7	2
	Irrigated land	4	55,028.5	36	5
	Buildings, edifices	4	16,461.6	16	3
	Orchard	3	356,890.5	23	3
Meso-Mediterranean (600–1350 m)	Grass land	2	31,690.6	13	5
	Shrub	2	380,320.2	86	6
	Evergreen oak forest	2	49,375.9	37	4
	River gallery	2	540.4	44	5
	Pine stand	3	165,487.1	43	7
	Cereal crop	3	391,567.8	82	4
	Irrigated land	4	80,758.4	107	5
	Buildings, edifices	4	22,524.7	58	4
	Orchard	3	379,769.7	129	6
Supra-Mediterranean (1350–2000 m)	Grass and shrub land	1	174,415.8	53	7
	Evergreen and oak forest	1	11,232.0	23	5
	River gallery	1	146.8	16	6
	Pine stand	2	100,988.2	35	7
Oro-Mediterranean (2000–2900 m)	Pine stand	2	5,498.4	3	2
	Grass and shrub land	1	26,611.6	10	4
Cryoro-Mediterranean (2900–3481 m)	Grass and shrub land	1	3,888.0	2	2

Mediterranean bioclimatic thermotypes follow Rivas-Martínez’s (1987) classification. Each habitat includes number of citations and snake species found in them, surface area (from Junta de Andalucía 1999), and the alteration level due to human factors [from pristine habitats (1) to extremely altered ones (4)]. See text for details.

in the study zone was calculated by ArcView 3.2 (Table I) based on the Junta de Andalucía (1999) software. According to the degree of human alterations, habitats were also classified into four levels (Table I): (1) pristine or unaltered habitats; (2) habitats with little modification; (3) habitats with considerable human impact, especially caused by agricultural activities; (4) habitats extremely altered due to irrigated crops and human constructions.

Data collection

Habitat data were recorded for 881 snakes, for eight out of the nine snake species inhabiting the south-eastern Iberian Peninsula (seven Colubridae and one Viperidae). *Natrix maura* (Linnaeus, 1758), probably the most common snake in Spain, was excluded from our study because of its aquatic habits. Field sampling was conducted from 1983 to 2004, within the framework of a larger study on the snake fauna of the region (details in Feriche 1998). We performed searches two to four field days per month (each about 6 h long), throughout all months of the year, within all the habitats of the study area, on the basis of a rather stratified sampling effort. For each observation, we recorded the variables snake species, habitat, and altitude (m a.s.l.). Although reproductive condition would have

an effect on microhabitat use (Reinert 1993), we did not differentiate between sex and/or reproductive condition of the individuals, as our habitat classification was on a coarse scale (macrohabitat level, *sensu* Orians and Wittenberger 1991), and the species considered here exhibit very small home ranges (personal observations).

Statistical procedures

For each snake species, we calculated the diversity of habitat use by the Shannon's Index (H'). Principal components analysis (PCA) was used to classify the snake species in terms of their similarities in habitat use in the study area. The loading scores on the first two extracted principal components were used as a measure of the association between snake species and habitat occupancy. The total variance accounting for each eigenvalue was used to evaluate the level of explanation of the analysis. Five variables were chosen to perform the PCA, as these variables are related to the amplexness of habitats used by each snake species: number of citations; number of UTM 10×10 km squares with citations in the study area (from data in the Atlas of amphibians and reptiles of Spain by Pleguezuelos et al. 2002); altitudinal range of citations; number of habitats occupied; and diversity value.

Results

During the study period, snake specimens were found in all Mediterranean bioclimatic thermotypes, Thermo-, Meso-, Supra-, Oro-, and Cryoro-Mediterranean. The number of citations increased according to the extension of the bioclimatic thermotypes (Kendall tau test = 1.0, $P = 0.01$, $n = 5$), suggesting an apparently homogeneous distribution of snakes in the study area. According to the alteration level of each habitat, only 11.6% of citations referred to natural pristine habitats, 27.8% to habitats with low alteration, 36% to medium alteration, and 24.6% to high alteration (Table II). However, taking into account the surface occupied by habitats grouped according to their alteration level, the number of citations was not correlated with the surface of each area (Kendall tau test = 0.67, $P = 0.17$, $n = 4$). Snakes were found in all types of habitats considered here, although there were sharp differences in the number of citations among them (Table I).

Table II. Mediterranean bioclimatic thermotypes (Rivas-Martínez 1987) and the four levels of habitat alteration in the study area (south-eastern Iberian Peninsula), with indication of the surface area occupied and snake records in each class.

	Surface (ha)	Citations
Bioclimatic thermotypes		
Thermo-Mediterranean	657,566	142
Meso-Mediterranean	1,502,035	599
Supra-Mediterranean	286,783	127
Oro-Mediterranean	32,110	13
Cryoro-Mediterranean	3,888	2
Habitat alteration		
Pristine natural habitats	216,294	104
Low alteration	678,187	245
Medium alteration	1,413,127	317
High alteration	174,773	217

See Material and methods section for details.

Table III. Use of altered and non-altered habitats of snake species in the south-eastern Iberian Peninsula

Snake species	Number of citations	Citations in unaltered habitats	Citations in altered habitats	χ^2 (P)
<i>Coronella austriaca</i>	5	5*	0	4.29 (0.04)
<i>Coronella girondica</i>	64	54*	10	31.32 (0.00001)
<i>Hemorrhois hippocrepis</i>	172	31	141*	14.16 (0.0002)
<i>Malpolon monspessulanus</i>	329	107	222	0.82 (0.4)
<i>Macroprotodon brevis</i>	30	21*	9	6.70 (0.01)
<i>Natrix natrix</i>	9	5	4	0.25 (0.6)
<i>Rhinechis scalaris</i>	238	89	149	0.08 (0.8)
<i>Vipera latastei</i>	36	34*	2	25.36 (0.00001)

χ^2 test is for the acceptance of the hypothesis that the number of observations is proportional to the extension of altered and unaltered habitats in the study area. In species with significant differences, an asterisk indicates habitats where the species were significantly more observed.

Among snake species, there was strong contrast in the number of citations in the study area (Table III), some snakes being very common [*Malpolon monspessulanus* (Hermann, 1804), *Rhinechis scalaris* (Schinz, 1822)] and others very scarce [*Coronella austriaca* Laurenti, 1768, *Natrix natrix* (Linnaeus, 1758)]. In most species, the occurrence in altered versus unaltered habitats did not follow a distribution related to the available surface area of both types of habitat: *Hemorrhois hippocrepis* (Linnaeus, 1758) was more common in altered habitats, whereas *C. austriaca*, *Coronella girondica* (Daudin, 1803), *Macroprotodon brevis* (Günther, 1862), and *Vipera latastei* Boscá 1878 were most common in unaltered habitats (Table III).

The scores for diversity in habitat-use frequency varied among the species (Table IV). The relation between the diversity values and the log-transformed number of citations for each species in the study area (Figure 1) showed that the commonest species had the highest diversity of habitat use (Kendall tau test = 0.86, $P = 0.003$, $n = 8$). In Figure 1, *C. austriaca* looks like an outlier as it is very scarce in the study area and confined to the top of some mountain chains (Galán 2002). *Vipera latastei* showed a low diversity score in relation to its abundance, whereas *C. girondica*, *M. brevis*, and *N. natrix* apparently had high diversity scores compared to the number of individuals found in the study area.

Table IV. Altitudinal range, number of habitats, and diversity scores in habitat use for snake species in the study area (south-eastern Iberian Peninsula).

Snake species	IUCN category		Altitudinal range (m)	Number of habitats	Diversity index, H'
	Spain	Andalusia			
<i>Coronella austriaca</i>	LC	EN	2100–2700	2	0.5
<i>Coronella girondica</i>	LC	NE	120–2250	15	2.31
<i>Hemorrhois hippocrepis</i>	LC	NE	1–1800	20	2.48
<i>Macroprotodon brevis</i>	NT	DD	30–1600	14	2.28
<i>Malpolon monspessulanus</i>	LC	NE	5–1980	21	2.63
<i>Natrix natrix</i>	LC	NT	5–3000	8	1.91
<i>Rhinechis scalaris</i>	LC	NE	5–1950	22	2.56
<i>Vipera latastei</i>	NT	VU	800–2950	8	1.63

For each species, the Spanish (Pleguezuelos et al. 2002) and Andalusian (Franco and Rodríguez de los Santos 2001) IUCN categories are included (applied at regional level): NE, Not Evaluated; LC, Least Concern; DD, Data Deficient; NT, Near Threatened; VU, Vulnerable; EN, Endangered.

Figure 1. Relationship between the diversity scores in habitat use and the number of citations (log transformed) for each snake species in the study area. Each point is one snake species: Ca, *Coronella austriaca*, Cg, *Coronella girondica*, Hh, *Hemorrhois hippocrepis*, Mb, *Macroprotodon brevis*, Mm, *Malpolon monspessulanus*, Nn, *Natrix natrix*, Rh, *Rhinechis scalaris*, VI, *Vipera latastei*.

The variance accounting for the two most explicative factors on the PCA was 73.28% and 20.11% (Figure 2). According to the PCA result, the snake species in the south-eastern Iberian Peninsula were classified in three main groups: (1) *H. hippocrepis*, *M. monspessulanus*, and *R. scalaris* exhibit the highest values in number of citations, number of habitats occupied, and habitat diversity (Table IV), and can be catalogued as generalists in the use of habitats in the study area; (2) *C. girondica*, *M. brevis*, *N. natrix*, and *V. latastei* appear to be a more heterogeneous group, although the four species are scarce in the study

Figure 2. Principal components plot for different snake species. The percentage of the variance explained by the two main factors is indicated on the axes. Three separate groups of species are indicated. Ca, *Coronella austriaca*, Cg, *Coronella girondica*, Hh, *Hemorrhois hippocrepis*, Mb, *Macroprotodon brevis*, Mm, *Malpolon monspessulanus*, Nn, *Natrix natrix*, Rs, *Rhinechis scalaris*, VI, *Vipera latastei*.

area and are almost restricted to unaltered habitats; (3) *C. austriaca* is the scarcest species in the study area, being present only in pristine mountain-top habitats above 2100 m altitude.

Discussion

This study clearly differentiates snake species inhabiting the southern Iberian Peninsula in terms of their habitat occupancy, distinguishing generalists from specialists. In the study area, the distribution of the snake community according to Mediterranean bioclimatic thermotypes seems to be homogeneous. However, when species were analysed separately, we found differences in the altitudinal range; some species are restricted to mountainous areas whereas others are distributed from coastal to medium mountainous areas (Table IV). Snake species also diverge in the occupancy of habitats according to alteration induced by humans; some species are almost restricted to unaltered habitats, usually confined to mountainous areas (e.g. *C. austriaca*, *V. latastei*), others show no differences in the occupancy of habitats classified according to their degree of alteration, and surprisingly *H. hippocrepis* appears to select altered habitats (Table III). The species in the last two categories show the highest diversity scores in habitat use (Table IV), and could take advantage of occupying altered habitats, as they are the most common species in the study area (Table III).

The study area is composed of several isolated mountains (locally called “sierras”) surrounded by wide valleys. In the sierras, natural habitats have been little affected by human activity. On the contrary, the original landscape in valleys has been intensely altered by humans, and it is currently comprised of small patches of natural and semi-natural Mediterranean forest and scrubland vegetation mixed with extensive cultivated areas of cereals, olive trees, and irrigated lands. The snake species that inhabit the altered habitats in valleys (*H. hippocrepis*, *R. scalaris*, *M. monspessulanus*) show a wide ecological niche use that includes high diversity of habitats (this study), and also a broad prey spectrum (Pleguezuelos 2003, 2006; Feriche 2004). This is the case for *M. monspessulanus*, a species frequently found in orchards and vineyards in several parts of its Iberian range (Busack and Jaksic 1982; Monrós 1997), or *H. hippocrepis*, a species that is frequently observed within urban areas in the study region (Feriche 2004). As predators, snakes tend to occupy areas with high prey density (Luiselli 2006). Thus, habitat selection in snakes is strongly correlated with habitat selection by their prey (Shine and Lambeck 1985), and therefore species with high diversity of habitats would be expected to exhibit a wide prey spectrum, as occurs in the commonest species in the study area (Pleguezuelos 2003, 2006; Feriche 2004). Furthermore, these species show low risk of population decline according to their intrinsic factors (Santos et al. 2007a). In this sense, *M. monspessulanus* was the only species found among all occupied habitats, the most generalist in prey-type consumption, and the species with the highest reproductive frequency in the study area (Feriche 1998). Habitat generalism is considered to be an important characteristic determining the ability of a species to remain in an area following fragmentation (Kjoss and Litvaitis 2001; Filippi 2003). Because *M. monspessulanus* is the most generalist species within the snake community of the study area, it appears not to be as sensitive to habitat alteration as the other snake species. In fact, during the last 20 years, this species has undergone a population increase in the study area, as opposed to the other snake species that appear to show a decline (C. Segura et al., unpublished data).

According to the use of habitats, generalist species apparently do not have conservation problems in the study area, in agreement with their plasticity in the use of ecological

sources (i.e. habitat occupancy and prey foraging). On the contrary, conservation concerns exist for rare and specialized species (Table III). It is suggested that these species tend to disappear with habitat loss, whereas common and versatile species would increase in abundance (Gray 1989). The application of the Filippi and Luiselli (2000) method to snakes in the southern Iberian Peninsula supports this idea: species with the highest risk of population decline are also scarce and occupy a low number of habitats (Santos et al. 2007a; Table IV). However, these species differ in their conservation problems. Some species (*C. girondica* and *M. brevis*) have probably disappeared or declined in altered habitats due to specialization in several life-history traits, such as feeding ecology (Luiselli et al. 2001 for *C. girondica*; Pleguezuelos et al. 1994 for *M. brevis*), or low reproductive frequency (Pleguezuelos and Feriche 1998). These species have been observed in rather numerous habitats in the study area, although the number of records is very low. Abundance of these species in other well-preserved areas (e.g. Maghreb mountains for *C. girondica*, south-western Iberian Peninsula for *M. brevis*; C. Segura et al., unpublished data) suggest a declining population in the study region because of human-related alterations that perhaps also affect their prey. For other snake species, rarity may be related to suboptimal habitat characteristics at their southern distribution limits (Santos et al. 2002, 2007a for *N. natrix*; authors, unpublished data for *C. austriaca*). The status for the latter species in the southern Iberian Peninsula is dramatic, as its distribution is restricted to small, isolated populations, often in the highest areas of several mountain chains (Galán 2002). However, the extinction of *C. austriaca* in lowland areas can be attributed to climatic constraints in addition to habitat alteration by humans. The extreme scarcity and restricted distribution of *C. austriaca* in the southern Iberian Peninsula explains its differentiated classification in the PCA (Figure 2).

After *C. austriaca*, *V. latastei* is the species with the lowest diversity index in habitat use in the study area, as it was found only in eight out of 24 habitats (Table IV). This apparent specialization contrasts with its wide tolerance with respect to the variables rainfall and altitudinal range in the Iberian Peninsula (Santos et al. 2006). In fact, the current distribution of *V. latastei* in the Iberian Peninsula is constrained by human activities in a way similar to other European vipers (Luiselli and Capizzi 1997; Filippi and Luiselli 2000). Several life-history traits of this species (sit-and-wait foraging tactic, female reproduction on triennial basis) increase its proneness to extinction (Santos et al. 2006, 2007b; Pleguezuelos et al. 2007), *V. latastei* becoming the most threatened species among Iberian snakes (Santos et al. 2007a).

Specialization in the use of habitats appears to be linked to the conservation status of the southern Iberian snake species. Generalist species are common and apparently without conservation concern, exhibiting good adaptability to altered habitats. Specialist species are threatened, probably by human alteration of the landscape. Evidently, this apparent association is also related to several biological traits that make some species more vulnerable to extinction than others (e.g. reproductive frequency, feeding specialization, etc.; Bennett and Owens 2002; Webb et al. 2002). In the study area, snake-species richness is higher in meso- and supra-Mediterranean thermotypes, which roughly define the medium-mountain areas (600–2000 m a.s.l.; Rivas-Martínez 1987; Table I), where habitat destruction is still low. Most of these areas are currently declared Natural and National Parks in the southern Iberian Peninsula. We consider the protection of these areas to be a good measure to maintain snake diversity in the study area, as some species of this reptile group are very vulnerable to habitat alteration (Filippi and Luiselli 2000; Santos et al. 2007a). Of the eight snake species here considered, only *V. latastei* and *C. austriaca* are

considered threatened at the regional level (Vulnerable and Endangered, respectively; IUCN categories; Franco and Rodríguez de los Santos 2001), and none at national level (Pleguezuelos et al. 2002). However, our results suggest that other species would be threatened (*C. girondica*, *M. brevis*, *N. natrix*), at least at regional and/or national level, and their conservation status urgently needs to be re-assessed in order to design suitable programmes for conservation management. The importance of this result derives from the fact that Spain holds most of the global distribution of many of the species considered here (*C. girondica*, *H. hippocrepis*, *M. monspessulanus*, *M. brevis*, *R. scalaris*, *V. latastei*), and therefore bears the brunt of the responsibility for their conservation at a global scale.

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