Smooth snakes at an Iberian mountain isolate and the relationship with competing southern smooth snakes

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Smooth snakes (*Coronella austriaca*) confined to cold-humid environments in Iberian high mountains may be threatened by the effects of climate warming, such as the expansion uphill of competing southern smooth snakes (*C. girondica*), but demographic studies allowing the assessment of population tendencies are lacking. Here, we determined the distributions and abundances of both species at Serra da Estrela based on records over 18 years (1993–2010). Smooth snakes comprised an isolated population at altitudes above 800 m. Abundances were highest above 1300 m, with densities of about one smooth snake per hectare above 1580 m. The distributions of the two species overlapped at altitudes of about 800–1600 m. We did not find any evidence for range shifts, or changes in smooth snake abundance over the past 18 years. Sex ratios were even, and high dietary specialization may contribute to the species' vulnerability. Efforts to conserve the smooth snake at Serra da Estrela should encompass studies aiming to improve knowledge of the species' demography, as well as continued monitoring to evaluate potential threats posed by climate warming. Our study may provide a baseline tool for future research on this poorly known snake.

Key words: abundance, conservation, *Coronella austriaca*, *Coronella girondica,* distribution

INTRODUCTION

Mountain ecosystems support a large fraction of the world's biological diversity, host evolutionarily unique and species-rich assemblages, and provide a wealth of ecological services and natural resources to humans (Diaz et al., 2003). However, they are also highly vulnerable to anthropogenic habitat degradation and are at risk for biodiversity loss due to global climate warming (Nogués-Bravo et al., 2007; Sorte & Jetz, 2010). To keep up with increasing temperatures, many species have already shifted their ranges towards higher latitudes and altitudes (Parmesan, 2006; Parmesan & Yole, 2003; Root et al., 2003). Montane species are becoming increasingly confined to mountain tops (Colwell et al., 2008; Wilson et al., 2005), and many are at risk of becoming extinct because of decreased ranges, altitudinal limits and low population sizes (Harris & Pimm, 2007; Schoo et al., 2005; Sekercioglu et al., 2008), and because suitable habitats will disappear (Benning et al., 2002; Williams et al., 2003). In addition, extinction of montane populations due to competitive exclusion and disease caused by invading low-altitude species is already widespread (Benning et al., 2002; Pounds et al., 2006; Sinervo et al., 2010).

The Serra da Estrela is located at the west tip of the Iberian Central Cordillera (40°20´N, 7°35´W) and is the highest mountain in continental Portugal. It shows stair-like plateaux between 1400 m above sea level and the summit (Torre) at 1993 m, dominated by glacial erosional landforms (Vieira, 2008). Serra da Estrela is also an important condensation barrier to the moist air masses that enter the Iberian Peninsula from the Atlantic. The climate is characterized by dry warm summers and a wet cold season from October to May with frequent snowfall at higher altitudes (Vieira et al., 2005). The high plateaux host a rich assembly of plants and animals adapted to cold-humid environments, many of which are Iberian and local endemics (Jansen, 2002; Vieira et al., 2005). Among the reptiles, they harbour relict populations of the Iberian rock lizard (*Iberolacerta monticola*; Moreira et al., 1999) and the smooth snake (*Coronella austriaca*; Malkmus, 2008). These species became confined to high elevations during the Messinian desiccation of the Mediterranean Sea, and have persisted at Serra da Estrela, amongst other mountainous regions, throughout the glacial and interglacial cycles of the Quaternary (Arribas et al., 2006; Santos et al., 2008).

The smooth snake is a medium sized (up to 80 cm total length) nonvenomous ovo-viviparous colubrid with diurnal and rather secretive habits. It is widely distributed in Europe, and reaches its southwestern limits in Iberia where it shows a continuous distribution throughout the northern regions, with population isolates in the Portuguese Atlantic coast, central Portugal, and central and southern Spain (Gálan, 2002; Malkmus, 2008; see Gálan, 2009 for species review). Two subspecies are recognized based on morphological traits (Malkmus, 1995), and molecular evidence suggests that *C. a. acutirostris* is distributed in northwestern Iberia, whereas *C. a. austriaca* represents the remainder of the species' range (Santos et al., 2008). In northern Spain, smooth snakes are occasionally found in high numbers, and may be considered

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Table 1. Number of smooth snake (*Coronella austriaca*) observations and minimum number of individuals, based on number of days (hours) of field research and surveyed area in hectares at four study sites during 1993–1999 and 2008–2010.

		1993	1994	1995	1996	1997	1998	1999	2008	2009	2010
Lagoa	Days	17	8	23	8	12	22	8	9	16	6
	Hours	103	40	97	39	42	49	26	30	60	32
	Area	0.81	0.81	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44
	Obs.	1	1	4	4	3	0	1	2	0	1
	Ind.	1	1	3	2	3	0	1	1	0	1
Perús	Days	-	-	7	6	11	10	8	9	9	8
	Hours	-	-	36	27	37	42	27	33	39	28
	Area	-	-	0.64	0.64	0.64	0.64	0.64	0.64	0.64	0.64
	Obs.	-	-	0	2	0	0	2	0	1	2
	Ind.	-	-	0	2	0	0	2	0	1	1
Ski	Days	-	16	34	6	7	9	6	32	37	11
	Hours	-	87	152	30	26	39	20	90	163	38
	Area	-	0.64	0.64	0.64	0.64	0.64	0.64	0.64	0.64	0.64
	Obs.	-	3	7	0	0	1	0	3	0	0
	Ind.	-	1	3	0	0	1	0	2	0	0
Torre	Days	20	17	38	9	13	33	12	-	-	-
	Hours	107	104	162	33	49	117	30	-	-	-
	Area	0.4225	0.4225	0.4225	0.4225	0.4225	0.4225	0.4225	-	-	-
	Obs.	0	0	0	0	0	0	0	-	-	-
	Ind.	0	0	0	0	0	0	0	-	-	-

common (Galán, 2009). Santos et al. (2009) showed that populations in southern Iberia persist only as vulnerable small isolates confined to high elevations.

In the Baetic range, the smooth snake is rare and highly vulnerable to local extinction, partly due to low population densities and the effects of climate warming, including the uphill expansion of predators and competitors (Santos et al., 2009). The southern smooth snake (*C. girondica*), an oviparous species with a circummediterranean range and a widespread distribution in Iberia (Santos & Pleguezuelos, 2009), may constitute the main competitor of the smooth snake in Iberia (Santos et al., 2009). Both snakes feed mostly on small lizards and rodents (Gálan, 2009; Santos & Pleguezuelos, 2009) and, when they occur in close proximity, show highly overlapping trophic niches (Gálan, 1988). Concerns over the vulnerability of smooth snakes are reinforced by the recorded sharp decline in recent years of one population from southern England (Reading et al., 2010). The smooth snake is evaluated as Least Concern in Europe (Cox & Temple, 2009) and Spain (Gálan, 2002), and as Vulnerable in Portugal (Cabral et al., 2005). However, the assessment of smooth snake populations in Iberia is hampered by the lack of studies addressing the species' demography and, in particular, the relationship between its abundance and that of competing southern smooth snakes.

Here, we address whether the smooth snake at Serra da Estrela is threatened by the expansion of southern smooth snakes and, furthermore, aim to provide a baseline for future population monitoring. We determined the distributions and abundances of both snakes based on records between 1993 and 2010. We also characterized the smooth snake population structure and diet as main factors that can influence the species' vulnerability.

MATERIALS AND METHODS

Range and altitudinal distribution

Over the past 18 years (1993–2010), we have recorded the date and geographical coordinates of smooth snakes (n=124) and southern smooth snakes (n=27) at the Natural Park of Serra da Estrela and near surroundings, through repeated visits covering the entire extension of the Park and field research of quantified sampling effort (see below). Further records of smooth snakes (n=20) and southern smooth snakes (n=9) from the same period were compiled from Park surveys (Brito-Abreu et al., 1994; Paupério et al., 2005). To establish the distributions of the two species, and to examine the species' altitudinal distributions, relative abundances and altitudinal overlap, we mapped all records using a Geographical Information System. We tested whether the species shifted uphill in the past 18 years by dividing this time frame into two nine-year periods (1993–2001 and 2002–2010).

Abundance at study sites, along transects and on roads

Field research to measure snake abundances was conducted at four sites during 1993–1999 and 2008–2010 (see Table 1). Sites were located between 1580 and 1980 m, and consisted of square grids permanently marked on the ground to allow accurate determination of animal sight-

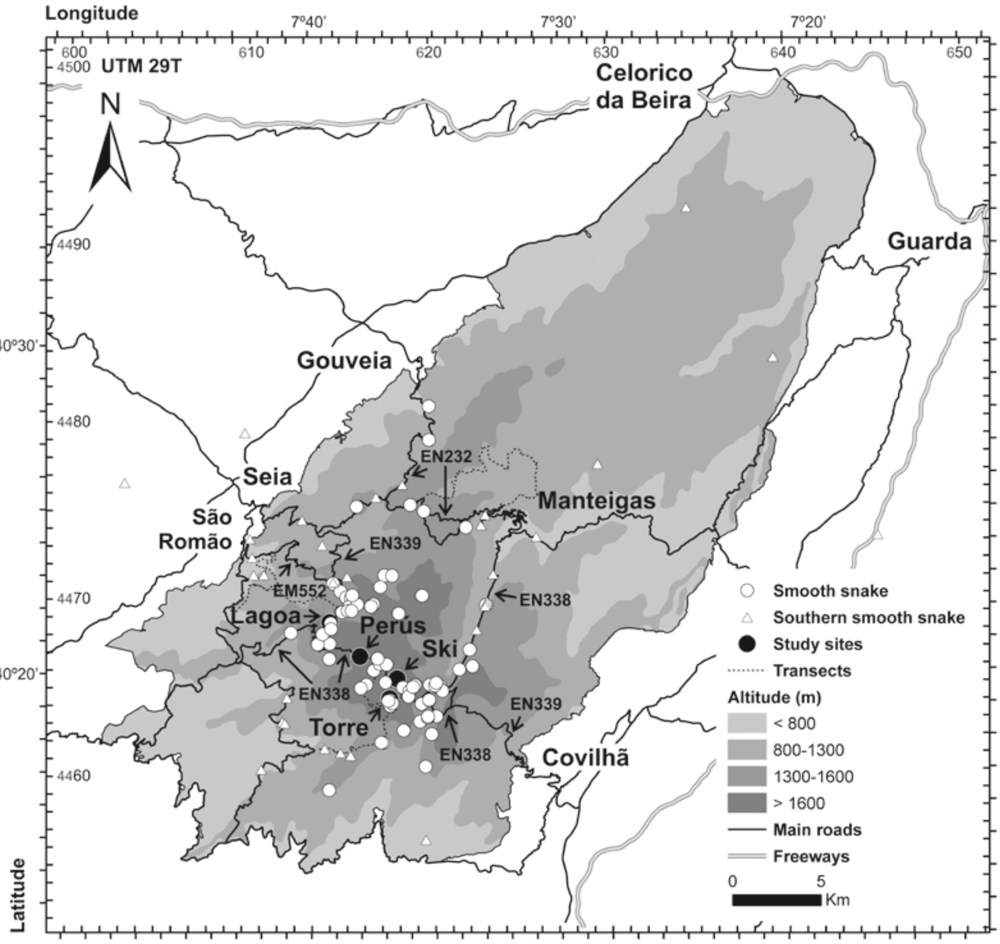

Fig. 1. Location of 144 smooth snake (*Coronella austriaca*) and 36 southern smooth snake (*C. girondica*) records at the Natural Park of Serra da Estrela and its surroundings. Multiple observations of the same species in the same locations are represented by a single point. Altitudes are represented within the boundaries of the Natural Park.

ing coordinates. "Lagoa" was located at 1580 m; the grid measured 50 × 50 m during 1993–1994 and was thereafter enlarged to 80 × 80 m. "Perús" was located at 1870 m and "Ski" at 1910 m and both measured 40 × 40 m. "Torre" was located at 1980 m (close to the mountain summit) and measured 25 × 25 m (site locations in Fig. 1). All sites were characterized by high rock cover, and shrub cover decreasing with altitude. Lagoa showed high cover of dwarf juniper (*Juniperus communis*), heath (*Erica* sp.) and broom (*Cytisus* sp. and *Genista florida*), Perús and Ski showed sparse junipers and heath, and Torre was devoid of shrubs. Fieldwork was conducted between March and September, following the emergence of reptiles from hibernation and before the return of winter conditions. The number of days (hours) of fieldwork differed between sites and years (see Table 1), with uniform surveying methods between sites and years. Researchers walked within 20 m from grid outer limits searching visually for snakes during a recorded time period (typically from 1000–1100 to 1800–1900 with a pause at midday; pauses were discounted from the quantification of sampling effort). The coordinates of all sightings of snakes and of two skin sheds were recorded. Captured snakes were identified (all were smooth snakes except one southern smooth snake at Lagoa in 1995), measured and weighed (as below), marked on the dorsal scales with acrylic paint for visual identification, and returned to capture locations the following day. Snake densities could not be estimated by capture–recapture methods due to scarcity of observations. Instead, we calculated the number of smooth snake observations (skin sheds excluded) per hour of fieldwork and area surveyed in hectares. In 80% of cases it was possible to distinguish between individual snakes, which differed in snout–vent length (SVL) and tail length (TL) in addition to the colour marks. Thus, we also calculated the number of different smooth snakes according to area surveyed in hectares. Snakes observed more than 20 m from the grid were excluded from the analyses. To examine whether smooth snake abundance varied spatially and temporally, we compared observations/hour/ha and smooth snakes/ha between sites and sampling periods.

Twenty-six transect walks were conducted along seven different routes (one route was conducted 10 times, one nine times, two twice and the remainder only once) at altitudes that ranged between 500 m and the mountain summit (see Fig.1). Transects were conducted on sunny

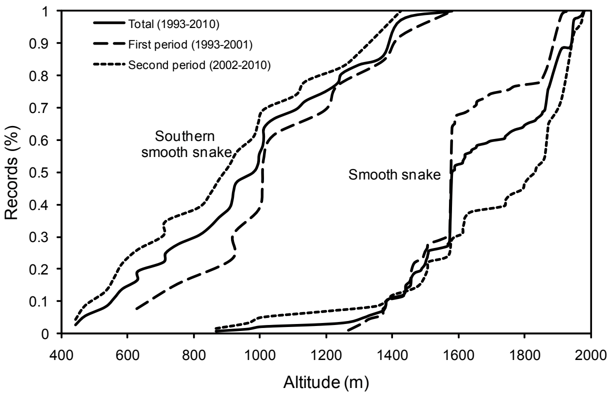

Fig. 2. Cumulative percentage of 144 smooth snake (*Coronella austriaca*) and 36 southern smooth snake (*C. girondica*) records according to altitude over the entire study period (1993–2010), and for two nine-year periods (1993–2001 and 2002–2010).

days from May to July between 2002 and 2007 and totalled 203 km. Observed snakes were captured, identified and released. Due to the limited number of observations, we pooled the data from all transects and calculated the number of observations according to the distance walked at four levels of altitude. These levels correspond to altitudes where only southern smooth snakes were recorded (<800 m), where both species were recorded but smooth snakes represented the minority (800–1300 m) or the majority (1300–1600 m) of records, and where only smooth snakes were recorded (>1600 m; see Fig. 3).

Road surveys were conducted during 1993–1999, 2004–2006 and 2008–2010 on sunny days between March and September along the EN-339, EM-552 and EN-338 that connect towns at the foothills of Serra da Estrela (Seia, São Romão and Manteigas; altitudes ranging from 500 to 700 m) to the mountain summit (see Fig. 1). These surveys took place over 12–94 days per year, and totalled 578 days and 13896 km. To quantify the abundance of both species, we pooled the data from all surveys and calculated the number of observations per 1000 km at each level of altitude. The surveys involved both directions at each day along the same road, but we only considered the distance travelled in one direction.

Smooth snake sex ratio, morphology and diet

Nineteen dead smooth snakes collected over the years were preserved in 70% alcohol. We recorded SVL and TL to the nearest 1 mm, head length to the nearest 0.1 mm and determined body mass to the nearest 0.001 g using a digital balance (100 g maximum capacity). Snakes were dissected and sexed by ascertaining the presence or absence of hemipenes and, when present, stomach contents were identified. Furthermore, 47 live smooth snakes were also measured, except that body mass was weighed to the nearest 0.1 g during 1993–1999 using a spring balance with 50 g maximum capacity (three males and one female weighed >50 g). Live snakes were bagged following capture and returned to capture locations the following day. When unforced regurgitation occurred, the diet remains were identified.

We used the observed sexual differences in TL/SVL among dead snakes (SVL >250 mm in all cases; one snake was excluded due to an incomplete tail) to sex live snakes with intact tails, with the exception of five juveniles (probably in their first year of life) with SVL <200 mm (Reading, 2004a). By pooling together data from dead and live snakes with assigned sex, we determined the population sex ratio (male/female) and tested for sexual differences in SVL, TL, body length (SVL+TL) and TL/SVL using snakes with intact tails (two were excluded). To test for sexual differences in head length and body mass, we used only live snakes because some dead snakes (mostly roadkills) had damaged heads.

RESULTS

Range and altitudinal distribution

Smooth snakes were not recorded below 800 m and southern smooth snakes were not recorded above 1600 m (Figs 1, 2). Smooth snake records ranged between 868 and 1980 m, and southern smooth snakes ranged between 442 and 1580 m; the altitude of records differed significantly between the species (Kolmogorov–Smirnov test, D=0.861, P<0001). At altitudes where the two species cooccurred (868–1580 m), the relative abundance of smooth snakes changed markedly with altitude (Fig. 3). Smooth snakes were found between 800 and 1300 m in 13–25% of their records (20% when pooling 100 m levels), with 80–98% of records between 1300 and 1600 m (92% when pooling 100 m levels; Fig. 3). There was no evidence for an uphill shift in the distribution of either of the

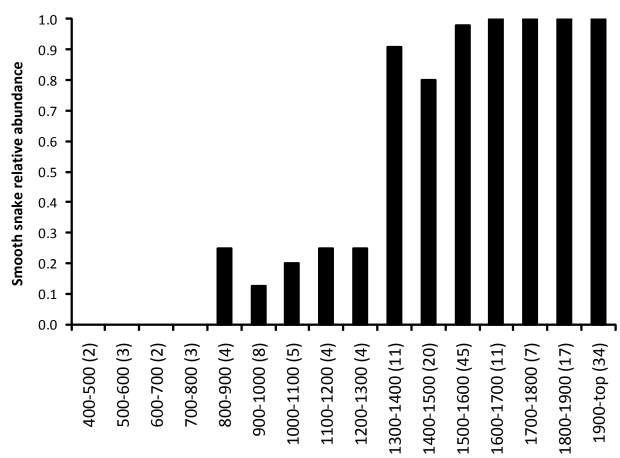

Fig. 3. Proportion of smooth snake (*Coronella austriaca*) records relative to total records of smooth snakes and southern smooth snakes (*C. girondica*) divided into 100 m altitude levels. Number of total records per altitude are indicated in brackets.

Table 2. Abundance of smooth snakes (*Coronella austriaca*) and southern smooth snakes (*C. girondica*) at four altitude levels based on data from transect walks (observations/1 km) and road travels (observations/1000 km). Distance covered and number of observations per surveying method are indicated.

	Transect walks					Road travels				
		Smooth snake		Southern smooth snake			Smooth snake		Southern smooth snake	
Altitude (m)	Dist. (km)	Obs.	Obs./1 km	Obs.	Obs./1 km	Dist. (km)	Obs.	Obs./1000 km	Obs.	Obs./1000 km
<800	12	0	0	0	0	954	0	0	1	1.05
800–1300	68	0	0	3	0.04	4748	2	0.42	2	0.42
1300–1600	34	1	0.03	0	0	3636	5	1.38	1	0.28
>1600	90	7	0.08	0	0	4558	6	1.32	0	0.00

species over the study duration. The relative abundance of smooth snakes at 800–1300 m (11% in 1993–2001 and 25% in 2002–2010) and at 1300–1600 m (95% in 1993–2001 and 81% in 2002–2010) did not differ significantly between the two periods of study (chi-square tests, 800–1300 m, χ^2=0.48, *P*=0.488; 1300–1600 m, χ^2=0.14, *P*=0.707). The altitude of smooth snake records differed significantly between 1993–2001 and 2002–2010 (Kolmogorov–Smirnov test, *D*=0.381, *P*<0001), but records at lower altitudes were more frequent in 2002–2010 than in 1993–2001 since four of five records below 1300 m (all roadkills) were made in 2002–2010 (Fig. 2). The altitude of southern smooth snake records did not differ significantly between the two periods (Kolmogorov–Smirnov test, *D*=0.368, *P*=0.164; Fig. 2).

Across the entire study area, the overlap between the altitudinal limits of the two species was 712 m. However, this value is highly influenced by low altitude (<1300 m) smooth snake records along the Zêzere river valley (along the EN-338 connecting Manteigas to the EN-339) and the north (along and to the north of EN-232) and by high altitude (>1300 m) southern smooth snake records in the northwest (along the EN-339 and EM-552 connecting Seia and São Romão to Lagoa). When examining specific areas of Serra da Estrela, the altitudinal overlap between species was much narrower. Along the Zêzere river valley, in the north and northwest respectively, the altitudinal limits of the two species overlapped by 102 m, 430 m and 229 m. In the south (area south of Torre), the two species did not overlap, and the lowest smooth snake record was 175 m higher than the highest southern smooth snake record.

Abundance

Altogether, 38 smooth snake observations were made at Lagoa, Perús and Ski; no snakes were observed at Torre (Table 1). Smooth snake observations averaged one observation/nine days or 38 hours of recording. The number of observations per year standardized by sampling effort (observations/hour/ha) was 0.031±0.024 at Lagoa, 0.048±0.056 at Perús and 0.024±0.030 at Ski. The differences between sites were statistically significant when all sites were considered (median test, χ^2=10.63, df=3, *P*=0.014), but not when Torre was excluded from the

Table 3. Morphological traits of juvenile, male and female smooth snakes (*Coronella austriaca*). Snout–vent length (SVL), tail length (TL), body length (SVL+TL) and TL/SVL were calculated for smooth snakes with intact tails (recorded dead and alive). Head length and body mass were calculated only for live snakes. *P*-values for t-tests on morphological sexual differences are shown.

	Juveniles					Males					Females					
	Mean	Min	Max	SD	*n*	Mean	Min	Max	SD	*n*	Mean	Min	Max	SD	*n*	*P*
SVL (mm)	188	178	200	9	5	435	250	560	85	30	462	290	620	83	29	0.229
TL (mm)	39	28	46	8	5	109	62	148	21	30	94	57	122	14	29	0.002
Body length (mm)	227	211	241	11	5	544	312	708	106	30	556	347	717	93	29	0.651
TL/SVL	0.207	0.140	0.242	0.044	5	0.251	0.234	0.273	0.011	30	0.206	0.152	0.233	0.023	29	<0.001
Head (mm)	8.6	8.3	9	0.4	5	13.7	10.2	16	1.6	21	12.8	10.2	15	1.5	20	0.232
Mass (g)	3.5	2.9	4.7	0.8	5	46.1	12	96	19.8	18	39.8	8.2	83	21.3	19	0.359

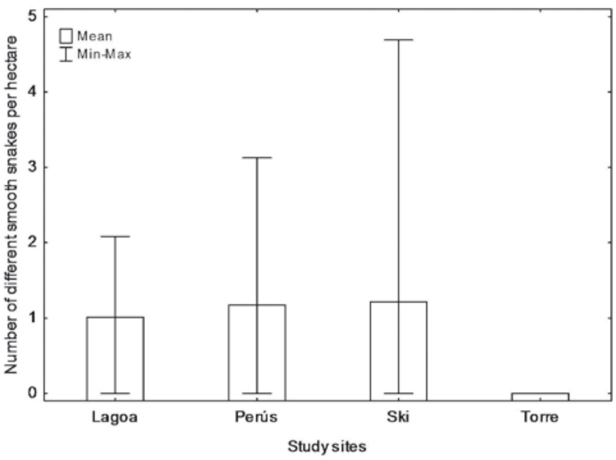

Fig. 4. Mean (minimum–maximum) number of smooth snakes (*Coronella austriaca*) observed per hectare at four study sites during the entire study period (1993–2010).

analyses (median test, χ^2=0.07, df=2, *P*=0.964). The 38 observations represented a minimum of 26 individuals (Table 1). The number of different smooth snakes per year at each site did not correlate positively with sampling effort expressed in days (Spearman rank order correlation, absolute r_s<0.59, *P*>0.127 in all cases) or hours (absolute r_s<0.58, *P*>0.103 at Lagoa and Ski and r_s=–0.69, *P*=0.056 at Perús), which suggests that sampling effort was large enough to detect most individuals. The number of smooth snakes/ha/year was 1.01±0.74 at Lagoa, 1.17±1.39 at Perús and 1.22±1.71 at Ski (Fig. 4). The maximum values of smooth snakes/ha across years were 2.08 at Lagoa, 3.13 at Perús and 4.69 at Ski (Fig. 4). The number of smooth snakes/ha differed significantly between sites when all sites were considered (median test, χ^2=10.63, df=3, *P*=0.014), but not when Torre was excluded from the analyses (median test, χ^2=0.07, df=2, *P*=0.964). The number of observations/hour/ha did not differ significantly between 1993–1999 and 2008–2010 at Lagoa, Perús and Ski (Mann–Whitney U test, *Z*<0.798, *P*>0.425 in all cases) and the number of smooth snakes/ha did not differ significantly between these periods (Mann–Whitney U test, *Z*<1.481, *P*>0.138).

Abundance along transects and on roads

Eight smooth snakes and three southern smooth snakes were recorded during 26 transect walks, and 13 smooth snakes and four southern smooth snakes (all roadkills) were observed during road surveys (Table 2). When examining snake abundances according to altitude levels, smooth snakes were more abundant above 1300 m, whereas southern smooth snakes were more abundant below 1300 m. Smooth snakes were three times more abundant above 1300 m than at 800–1300 m, and the abundance of southern smooth snakes decreased steadily with altitude (Table 2).

Smooth snake sex ratio, morphology and diet

Dead snakes that were sexed and had intact tails included nine males and nine females. TL/SVL ranged between 0.234 and 0.273 mm (0.253±0.013) among males, and 0.195 and 0.233 (0.218±0.015) among females. TL/SVL did not overlap between sexes and was significantly higher for males than for females (t-test, *t*=5.37, df=16, *P*<0.001). The highest value of TL/SVL observed among dead females (0.233) was used as the cut-off point to sex live adult snakes. Among the 19 dead and 41 live snakes that were sexed, 30 (50%) were males and 30 (50%) were females. Only TL and TL/SVL differed significantly between sexes, with males having both higher TL and higher TL/SVL than females (Table 3).

The diet was restricted to Iberian rock lizards and lacertid eggs. Among the dead snakes, one snake contained an adult gravid female with seven eggs and a juvenile, and another snake contained 16 eggs, possibly belonging to two clutches (11 eggshells in the upper region of the stomach and five further down). Regarding live snakes, two regurgitated the remains (tails and limbs) of Iberian rock lizards, and another regurgitated an entire adult. All dead and live specimens whose diet was determined were collected above 1400 m.

DISCUSSION

The smooth snake has a wide European distribution, but knowledge of the conservation status of its populations is scarce. This is certainly due to the species' secretive habits and typically low population densities (Goddard; 1984, Spellerberg & Phelps 1977), which render long-term individual-based demographic and behavioural field studies difficult to accomplish (but see Goddard & Spellerberg, 1980; Luiselli et al., 1996). Nonetheless, there is evidence that smooth snakes are declining, possibly due to climate warming (Reading et al., 2010; Santos et al., 2009). Here, we addressed whether smooth snakes at Serra da Estrela are threatened by the uphill expansion of competing southern smooth snakes and, furthermore, aimed to provide a baseline for future population monitoring.

Smooth snakes at Serra da Estrela are confined to altitudes above 800 m. The population is probably isolated by distances of more than 20–80 km to other mountains where the species was recorded (Malkmus, 2008); the lowlands surrounding Serra da Estrela are characterized by hot dry summers, seemingly unsuitable for smooth snakes (Santos et al., 2009). Despite low densities, this population may constitute an important reservoir of the species' genetic diversity as it is located at the southern limits of the distribution of *C. a. acutirostris* (Santos et al., 2008).

The distributions of both snake species overlap at altitudes of 800–1600 m overall, although the overlap only covered 102–430 m in altitude when different areas of

Serra da Estrela were examined. A narrow overlap between species may be indicative of on-going competitive exclusion due to, for instance, overlapping trophic niches (Gálan, 1988). However, our records include observations of both species in close proximity, thus raising the possibility that they coexist within such overlapping areas due to selection of different microhabitats (as reported for northern regions of Iberia, Gálan, 1988). Our results did not confirm that climate warming is driving the uphill expansion of southern smooth snakes at the cost of smooth snakes (Santos et al., 2009). In fact, we found no evidence for a range shift or changes in abundance for either species. Arguably, the time frame of our study is too short to evaluate the effects of climate warming on the species' altitudinal distributions, and only future population monitoring may comprehensively assess the risk of smooth snake extinction due to climate warming. Future population monitoring should preferably encompass the marking of individuals across a wider spectrum of altitudes and habitats. Current habitat degradation associated with recurrent fires and the construction of tourist facilities at high altitudes, as well as direct mortality arising from increased road traffic, are further threats to the viability of the smooth snake population at Serra da Estrela.

The abundances of both snakes varied markedly with altitude. Data from both transect walks and road surveys showed that smooth snakes are more abundant above 1300 m, whereas road observations indicate that smooth snakes are three times more abundant above 1300 m than at 800–1300 m. The three study sites where smooth snakes were recorded showed similar mean densities that ranged between 1.0 and 1.2 smooth snakes/ha, similar to values reported from southern England (0.92–1.99 snakes/ha; Goddard, 1984), lower than the densest reported populations (11–17 snakes/ha; Spellerberg & Phelps, 1977), and higher than at other isolates from southern Iberia (Sierra Nevada, one snake per 717 hours of fieldwork; Santos et al., 2009). Although we did not record smooth snakes at the highest altitude site during quantified visual surveys, smooth snakes were observed at the mountain top in other circumstances.

Despite small sample sizes, our results indicate that smooth snakes rely on a highly specialized diet that was restricted to Iberian rock lizards and lacertid egg clutches (possibly also those of Iberian rock lizards). Iberian rock lizards comprise the densest lizard populations where snakes with stomach contents were collected (personal observations), and a single prey item may increase the vulnerability of smooth snakes due to its availability (Reading, 2004b). Annual juvenile recruitment is apparently low, as we only captured five first-year juveniles (9% of all smooth snakes collected).

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REFERENCES

Arribas, O., Carranza, S. & Odierna, G. (2006). Description of a new endemic species of mountain lizard from northwestern Spain: *Iberolacerta galani* sp. nov. (Squamata: Lacertidae). *Zootaxa* 1240, 1–55.

Benning, T.L., LaPointe, D., Atkinson, C.T. & Vitousek, P.M. (2002). Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proceedings of the National Academy of Sciences, USA* 99, 14246–14249.

Brito-Abreu, F., Moreira, P.L., Rosa, H.D., Paulo, O.S. & Crespo, E.G. (1994). *Projecto de Estudo da Herpetofauna do Planalto Central da Serra da Estrela*. Final project report. Lisbon: Faculdade de Ciências da Universidade de Lisboa e Instituto da Conservação da Natureza.

Cabral, M.J. (coord.), Almeida, J., Almeida, P.R., Dellinger, T., Ferrand de Almeida, N., Oliveira, M.E., Palmeirim, J.M., Queiroz, A.L., Rogado, L. & Santos-Reis, M. (eds) (2005). *Livro Vermelho dos Vertebrados de Portugal*. Lisbon: Instituto de Conservação da Natureza.

Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C. & Longino, J.T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322, 258–261.

Cox, N.A. & Temple, H.J. (2009). *European Red List of Reptiles*. Luxembourg: Office for Official Publications of the European Communities.

Diaz, H.F., Grosjean, M. & Graumlich, L. (2003). Climate variability and change in high elevation regions: past, present and future. *Climatic Change* 59, 1–4.

Gálan, P. (1988). Segregación ecológica en una comunidad de ofidios. *Doñana, Acta Vertebrata* 15, 59–78.

Gálan, P. (2002). *Coronella austriaca* (Laurenti, 1968) Culebra lisa europea. In *Atlas y Libro Rojo de los Anfibios y Reptiles de España*, 272–274. Pleguezuelos, J.M., Márquez, R. & Lizana, M. (eds). Madrid: Dirección General de Conservación de la Naturaleza-AHE.

Gálan, P. (2009). Culebra lisa europea – *Coronella austriaca* Laurenti, 1768. In *Enciclopedia Virtual de los Vertebrados Españoles*. Salvador, A. & Marco, A. (eds). Madrid: Museo Nacional de Ciencias Naturales. Available at www.vertebradosibericos.org (accessed 7 December 2010).

Goddard, P. (1984). Morphology, growth, food habits and population characteristics of the smooth snake *Coronella austriaca* in southern Britain. *Journal of Zoology* 204, 241–257.

Goddard, P. & Spellerberg, I.F. (1980). Reproduction as a factor in the conservation of *Coronella austriaca* Laur. in southern England. *Bulletin d'Ecologie* 11, 535–541.

Harris, G. & Pimm, S.L. (2007). Range size and extinction risk in forest birds. *Conservation Biology* 22, 163–171.

Jansen, J. (2002). *Geobotanical Guide of the Serra da Estrela*. Lisbon: Instituto da Conservação da Natureza, Ministério das Cidades, Ordenamento do Território e Ambiente.

Luiselli, L., Capula, M. & Shine, R. (1996). Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps. *Oecologia* 106, 100–110.

Malkmus, R. (1995). *Coronella austriaca acutirostris* subspec.

nov aus dem Nordwesten der Iberischen Halbinsel (Reptilia: Serpentes: Colubridae). *Zoologische Abhandlungen Staatlinches Museum für Tierkunde Dresden* 48, 265–278.

Malkmus, R. (2008). *Coronella austriaca* (Laurenti, 1768) Cobra-lisa-europeia. In *Atlas dos Anfíbios e Répteis de Portugal*, 168–169. Loureiro, A., Ferrand de Almeida, N., Carretero, M.A. & Paulo, O.S. (eds). Instituto da Conservação da Natureza e da Biodiversidade, Lisboa.

Moreira, P.L., Almeida, A.P., Rosa, H.D., Paulo, O.S. & Crespo, E.G. (1999). *Bases para a Conservação da Lagartixa-da-montanha,* Lacerta monticola. Lisbon: Instituto da Conservação da Natureza, Estudos de Biologia e da Conservação da Natureza n. 25.

Nogués-Bravo, D., Araújo, M.B., Errea, M.P. & Martínez-Rica, J.P. (2007). Exposure of global mountain systems to climate warming during the 21st century. *Global Environmental Change* 17, 420–428.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37, 637–669.

Parmesan, C. & Yole, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.

Paupério, J., Grosso-Silva, J.M., Soares, C., Tarroso, P., Ferreira, S., Múrias dos Santos, A., Queiróz, N.,Godinho, R. & Alves, P.C. (2005) *Fomento e Caracterização de Presas Selvagens no Parque Natural da Serra da Estrela*. Relatório Final do Protocolo de Colaboração entre o ICN/PNSE e o CIBIO/ICETA-UP.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., Marca, E.L., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439, 161–167.

Reading, C.J. (2004a). Age, growth and sex determination in a population of smooth snakes, *Coronella austriaca* in southern England. *Amphibia–Reptilia* 25, 137–150.

Reading, C.J. (2004b). The influence of body condition and prey availability on female breeding success in the smooth snake (*Coronella austriaca* Laurenti). *Journal of Zoology* 264, 61–67.

Reading, C.J., Luiselli, L.M., Akani, G.C., Bonnet, X., Amori, G., Ballouard, J.M., Filippi, E., Naulleau, G., Pearson, D. & Rugiero, L. (2010). Are snakes in widespread decline? *Biology Letters* 6, 777–780.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60.

Santos, X., Brito, J.C., Caro, J., Abril, A.J., Lorenzo, M., Sillero, N. & Pleguezuelos, J.M. (2009). Habitat suitability, threats and conservation of isolated populations of the smooth snake (*Coronella austriaca*) in the southern Iberian Peninsula. *Biological Conservation* 142, 344–352.

Santos, X. & Pleguezuelos, J.M. (2009). Culebra lisa meridional – *Coronella girondica*. In *Enciclopedia Virtual de los Vertebrados Españoles*. Salvador, A. & Marco, A. (eds). Madrid: Museo Nacional de Ciencias Naturales. Available at www.vertebradosibericos.org (accessed 7 December 2010).

Santos, X., Roca, J., Pleguezuelos, J.M., Donaire, D. & Carranza, S. (2008). Biogeography and evolution of the smooth snake *Coronella austriaca* (Serpentes: Colubridae) in the Iberian Peninsula: evidence for Messinian refuges and Pleistocenic range expansions. *Amphibia–Reptilia* 29, 35–47.

Schoo, L.P., Williams, S.E. & Hero, J.M. (2005). Climate warming and the rainforest birds of the Australian Wet Tropics: using abundance data as a sensitive predictor of change in total population size. *Biological Conservation* 125, 335–343.

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008). Climate change, elevational range shifts and bird extinctions. *Conservation Biology* 22, 140–150.

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda, P.V., Rocha, C.F.D., Ibargüengoytía, N., Puntriano, C.A., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J. & Sites, J.W. Jr. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899.

Sorte, F.A. La & Jetz, W. (2010). Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society of London Series B* 277, 3401–3410.

Spellerberg, I.F. & Phelps, T.E. (1977). Biology, general ecology and behavior of the snake, *Coronella austriaca* Laurenti. *Biological Journal of the Linnean Society* 9, 133–164.

Vieira, G. (2008). Combined numerical and geomorphological reconstruction of the Serra da Estrela plateau icefield, Portugal. *Geomorphology* 97, 190–207.

Vieira, G., Jansen, J. & Ferreira, N. (2005). Environmental setting of the Parque Natural da Serra da Estrela. In *Landscape Ecology and Management of Atlantic Mountains*, 53–64. Pinto Correia, T., Bunce, R.G.H. & Howard, D.C. (eds). UK: International Association for Landscape Ecology, publication series no. 2.

Williams, S.E., Bolitho, E.E. & Fox, S. (2003) Climate change in Australian tropical rainforest: an impending environmental catastrophe. *Proceedings of the Royal Society of London Series B* 270, 1887–1892.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.L. (2005). Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* 8, 1138–1146.

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