Body size, diet and reproductive ecology of *Coluber hippocrepis* in the Rif (Northern Morocco)

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Abstract. Although it is generally assumed that the Horseshoe Whip Snake (*Coluber hippocrepis*) originated in northern Africa, its biology and ecology has been studied mainly in southern Europe. In this paper we report on morphology, feeding, and reproductive ecology of *Coluber hippocrepis* in the Rif region (northern Morocco). Males attained larger sizes than did females, but there was no body-size difference between populations separated by the Strait of Gibraltar. The species feeds exclusively on vertebrates: mammals (45%), reptiles (28%), birds (17%), and amphibians (10%). There was an ontogenetic dietary shift in terms of frequency of prey consumed and in terms of prey size; moreover, an intersexual difference in prey frequency was found. Sexual maturity was attained at 540 mm snout-vent length (SVL) in males, and 720 mm SVL in females. Males showed a vernal spermatogenic cycle. Oviposition occurred at the beginning of summer, and offspring were observed in the field during September.

Introduction

The Horseshoe Whip Snake (*Coluber hippocrepis*) is a terrestrial, slender-bodied colubrid distributed throughout northern Tunisia and Algeria, most regions of Morocco, both the eastern and southern half of the Iberian Peninsula, and some Mediterranean islands, such as Sardinia, Pantelleria, and Zembra (Schleich et al., 1996; Pleguezuelos, 1997). The wide distribution in northern Africa, the presence in that region of a very closely related species (*C. algirus*), and the possession by males of a vernal spermatogenic cycle (Pleguezuelos and Feriche, 1999), imply that the species probably originated in Africa (Pozuelo, 1974). It is generally assumed that this snake reached the Iberian Peninsula prior to the formation of the Strait of Gibraltar. However, to date, fossils of this species have been found on the northern side of the Strait only in relatively recent sediments (Bailón, 1991), and a

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small genetic distance separates the African and European populations (Busack, 1986). On Mediterranean islands, populations are thought to have originated from introductions in historical times (Bons and Geniez, 1996).

Most studies dealing with the natural history of this species concern the Iberian populations and those introduced on islands (i.e. Bruno and Hotz, 1976; Vericad and Escarré, 1976; Cattaneo, 1985; Meijide and Salas, 1987; Pleguezuelos and Moreno, 1990; Capula et al., 1997; Pleguezuelos and Feriche, 1999; Corti et al., 2000), while fewer concern the original populations from northern Africa (Bons, 1967; Hammer and Arlettaz, 1998). The existence of previous and current marine barriers in the Strait of Gibraltar provides a promising scenario to reconstruct the historical biogeography and evolution of this species and other reptiles in the western Mediterranean Basin (Busack, 1986; Caputo, 1993; Mateo et al., 1996; Alvarez et al., 2000; etc.). Indeed, when related populations or taxa occur on both sides of a long-standing barrier, differences should arise, not only at a molecular level, but also at an ecological level (Schwaner, 1985; Shine, 1987; Tanaka and Ota, 2002). Nevertheless, very few studies deal with shift in natural-history parameters of vertebrate populations separated by the Strait of Gibraltar (but see Busack and McCoy, 1990; Pleguezuelos et al., 1994).

In the present paper, we offer data on the natural history (morphology, feeding and reproductive ecology) of the Horseshoe Whip Snake in the Rif region (northern Morocco), in order to make comparisons between these populations and conspecific from north of the Mediterranean.

Material and methods

Study area

The Rif region (northern Morocco) occupies a geographical strip of about 27 900 km^2 close to the Mediterranean Sea. This strip is 90 km wide (34°15′-35°55′N) and 340 km long (2°19′-6°3′W). The climate ranges from Mediterranean to sub-Saharan; the Atlantic side of the region is characterised by rather heavy rainfall (annual average higher than 1000 mm), whereas on the Mediterranean side rainfall is around 400 mm, decreasing to less than 200 mm in some places in the Moulouya Basin. Temperatures in the northern zone, influenced by the Mediterranean Sea, are lower than in the southern zone, with a more continental climate (mean maximum temperature of the hottest month: Al Hoceima, 28.0°C versus Saka, 36.1°C; standard 30-year meteorological averages; Maurer, 1968). In terms of vegetation, the study area is among the most diversified in North Africa, although the autochthonous vegetation is rather degraded. The landscape is currently characterised by a mosaic of habitats, in general with shrub and pastures in the west, forests in the mountains of the central part, and arid steppes in the east (Benabid, 1985).

Sampling

The study was conducted from 1991 to 2000, throughout 14 expeditions, totalling 84 sampling days (three observers per day). The unit of sampling effort was established as one observer per biotope for 30 min. Random sampling to locate snakes was done throughout the study area, for a total of 1344 sampling units, with consistent effort over the year and across the years. When possible, specimens were captured by hand. No specimen was deliberately killed for the present study. However, most specimens were found dead (traffic casualties or killed by local people). Voucher specimens, preserved in alcohol, were deposited in the Faculty of Sciences of Tetouan (Morocco). As this study lasted for 10 years, we assumed that the seasonal activity and reproductive cycling of the species remains stable over the years.

Morphology, feeding and reproductive ecology

We examined 141 individuals (dead and alive). In all specimens, snout-vent and tail length (SVL, TL) were measured with a cord to the nearest mm, and biomass with an electronic balance to the nearest 0.1 gr. We assumed that linear measurements taken from live individuals were less precise that those taken from the voucher specimens; anyway, we pooled both set of data. Sex was determined by dissection in voucher specimens, and by the SVL/TL relationship and the shape of the tail in live individuals (Feriche et al., 1993). To get food data, live snakes were abdominally palpated to force regurgitation, and vouchers were dissected. The prey items were identified to the species level, but dietary comparisons of snakes north and south of the Mediterranean Sea were performed at the family level. The direction of prey ingestion was recorded, being inferred from the prey orientation within the gut. Only prey in good condition were weighed, after draining them on paper towel. Body length and weight of partially digested prey were estimated by comparison with conspecifics from the study area stored in the collection of the Faculty of Sciences at Tetouan. For the analysis of ontogenetic dietary shift, three SVL classes of snakes were considered: juveniles (Group I: $\mathrm{SVL} < 600$ mm), individuals approaching sexual maturity (Group II: $600 < \mathrm{SVL} < 800$ mm), and the largest individuals (Group III: $\mathrm{SVL} > 800$ mm). Food-niche breadth was calculated according to Shannon's index (Shannon, 1948); intersexual and inter-geographic overlap in diet composition was calculated by Pianka's symmetrical index (α_{jk}; Pianka, 1973); this index ranges between 0 (no overlap) and 1 (total overlap). To calculate the diet niche breadth and overlap, specimens without gut contents or with unidentified prey were not considered.

For the analysis of the reproductive ecology, the following measurements were taken: longest, medium, and shortest axes of the right testis (larger than the left one) in males (±0.1 mm), diameter of the largest ovarian follicle or oviductal egg (±0.1 mm) in females, and fat body level in both sexes. Several specimens were road-killed, and some of them were damaged. Thus, measurements were taken only from organs in good condition. The fat-body level was scored in five visual categories; from zero (no traces of fat) to four (a continuous fat layer in the ventral zone of the abdominal cavity (details in Pleguezuelos and Feriche, 1999)). In males, the size at maturity and the spermatogenic cycle was determined relating the testicular volume (TV) with the spermatogenic activity (Seigel and Ford, 1987). TV was estimated using the formula for the volume of a flattened ellipsoid. Because TV increases significantly with SVL, the ratio of right-testis volume/cubic SVL (relative testicular volume, thereafter RTV) was used to determine graphically maturity and the spermatogenic cycle. The reproductive condition in females was established according to the presence of vitellogenic follicles in ovaries as well as oviductal eggs. Clutch size was determined counting eggs in the oviducts or enlarged follicles (larger than 15 mm in maximum diameter). For establishing the frequency of reproduction, the proportion of mature gravid females during the period of reproduction was considered. As this frequency may be biased if pregnant females change their behaviour with respect to adult non-reproductive ones (reproductive females spend more time above-ground), we realize that the method may overestimate the results (Bonnet and Naulleau, 1996). Hatching time was estimated on the basis of the appearance of neonates in the field surveys. Means are followed by $\pm \sigma$. ANOVA were used after testing data for normality and equality of variances. When possible ANCOVA was used, and the parallelism and homoscedasticity of both distributions was previously tested; when linear variables (SVL) were correlated against ponderal ones (biomass), logarithmic reduction was performed. The level of significance was set at 5%. Data for comparisons with populations in southern Spain (thereafter, the Baetic population) were obtained from Feriche (1998), Pleguezuelos and Feriche (1999) (body size, reproductive traits) and Pleguezuelos and Moreno (1990) (feeding habits).

Results

Body size, sexual dimorphism and sex ratio

SVL of the snake sample ranged from 243-1371 mm ($\bar{x} = 712.3 \pm 305.6$ mm). Body-size difference between populations of Morocco and southern Spain was almost significant (ANOVA, $F_{1,416} = 3.44$, $P = 0.06$). Restricting comparisons of SVL to the 10 largest specimens in each population (see Schwaner and Sarre, 1988), it resulted that the Moroccan and Spanish populations were practically identical (ANOVA, $F_{1,18} = 0.000$, $P = 0.99$).

All specimens were accurately sexed. Adult sex-ratio (males : females, 1.12 : 1, $n = 141$) did not differ from equality (2 × 2 Contingency Table, $\chi^2 = 0.23$, $P = 0.63$), and was quite similar to that found in the south-eastern Iberian Peninsula ($\chi^2 = 0.15$, $P = 0.69$). Males attained significantly larger sizes ($\bar{x} = 825.1 \pm 315.7$ mm, $n = 73$) than females ($\bar{x} = 592.4 \pm 256.1$ mm, $n = 50$; ANOVA, $F_{1,122} = 18.97$, $P < 0.000$). The maximum SVL attained by males was 1371 mm versus 1284 mm in females.

Table 1. Composition of the diet of *C. hippocrepis* in the Rif.

	Males ($n = 74$)		Females ($n = 66$)		Total ($n = 141$)	
	Frequency	Prey-mass (%)	Frequency	Prey-mass (%)	Frequency	Prey-mass (%)
AMPHIBIANS						
Discoglossus pictus	2	0.2			2	0.1
Rana saharica	1	1.4	2	1.9	3	1.7
REPTILES						
Tarentola mauritanica	1	1.5	1	1.0	2	1.2
Saurodactylus fasciatus			2	0.2	2	0.1
Agama bibroni			1	9.7	1	5.6
Podarcis hispanica	3	1.6	5	2	8	1.8
Psammodromus algirus			2	0.3	2	0.2
BIRDS						
Passer domesticus	2	10.6	7	26.5	9	19.9
MAMMALS						
Suncus etruscus	1	1.4	1	0.5	2	0.9
Oryctolagus cuniculus	1	26.1			1	10.8
Apodemus sylvaticus	4	15.1	2	6.6	6	10.1
Lemniscomys barbarus	1	3.1	2	4.4	3	3.9
Rattus rattus	2	24.3	2	37.6	4	32.0
Rattus norvegicus	1	3.1			1	1.3
Mus musculus					1	1.3
Mus spretus	2	8.9	1	2.1	3	4.9
Mus sp.	1	2.6	2	4.8	3	3.9
AMPHIBIANS	3	1.7	2	1.9	5	1.8
REPTILES	4	3.1	11	13.2	15	9
BIRDS	2	10.6	7	26.5	9	19.9
MAMMALS	13	84.5	11	58.5	24	69.4
Diet diversity (H′)	2.44		2.44		2.54	

Diet

Of the 141 guts examined, 46 contained prey (32.6%). Among the specimens with prey, most had a single prey (89.0%), four had two, and only one had four prey (three chicks of *Passer domesticus* and one *Mus musculus*). The species feeds exclusively on vertebrates, mostly on mammals, followed in frequency by reptiles, birds, and amphibians (table 1). The relative importance of the amphibians in the diet is noteworthy in terms of number of prey items, but, as usual in studies of the feeding habits of generalist snakes, an analysis of the biomass which each prey contributes to diet significantly increases the importance of endotherms (89.2%) with respect to ectotherms (10.8%; table 1).

Snakes consumed prey ranging in size from 17 to 262 mm body length, extremes represented by *Discoglossus pictus* and *Rattus norvegicus*, respectively. Mean prey size was 77.7 mm (±50.7, $n = 53$) in the Rif, which significantly exceeds the mean prey size in the Baetic population (ANOVA, $F_{1,189} = 6.87$, $P < 0.009$; see table 3). Mean relative prey length was 0.101 (±0.045, $n = 53$). Prey biomass ranged between 0.8-212.0 gr,

Table 2. Ontogenetic variation of the composition of the diet of *C. hippocrepis*.

	Group I SVL < 600 mm ($n = 50$)		Group II 600 < SVL < 800 mm ($n = 23$)		Group III SVL > 800 mm ($n = 64$)	
	Frequency	Prey-mass (%)	Frequency	Prey-mass (%)	Frequency	Prey-mass (%)
AMPHIBIANS						
Discoglossus pictus	2	1.4				
Rana saharica			2	4.0	1	0.7
REPTILES						
Tarentola mauritanica			1	2.1	1	0.9
Saurodactylus fasciatus	2	1.4				
Agama bibroni			1	19.4		
Podarcis hispanica	8	26.7				
Psammodromus algirus	2	2.8				
BIRDS						
Passer domesticus			3	26.9	6	28.7
MAMMALS						
Suncus etruscus	1	4.2				
Oryctolagus cuniculus					1	14.9
Apodemus sylvaticus			3	17.9	3	6.8
Lemniscomys barbarus	1	17.8	1	4.7	1	1.8
Rattus rattus			1	16.7	2	34.6
Rattus norvegicus			1	4.4		
Mus musculus	1	27.9			1	2
Mus spretus	1	17.8			2	5.1
Mus sp.			1	3.8	2	3.9
AMPHIBIANS	2	1.4	2	4.0	1	0.7
REPTILES	12	31	2	21.5	1	0.9
BIRDS	0	0	3	26.9	6	28.7
MAMMALS	4	67.6	7	47.5	12	69.7

extremes represented by *Podarcis hispanica* and *R. norvegicus*, respectively. Mean prey biomass was 24.2 gr (±39.0, $n = 53$) which also exceed significantly mean prey mass of the Baetic population (ANOVA, $F_{1,130} = 6.05$, $P < 0.01$). Mean relative prey mass was 0.143 (±0.150, $n = 53$).

For comparing the diet between the populations separated by the Strait of Gibraltar, and because of statistical constraints, the number of different prey was reduced to only seven prey types: i) geckos, ii) lacertids, iii) other reptiles, iv) birds, v) large micrommals (*Rattus*, *Oryctolagus*), vi) small micromammals (*Suncus, Lemniscomys, Mus, Apodemus*), vii) other prey (invertebrates, amphibians). Diets differed between the two populations (G-test = 21.1, df = 6, $P < 0.001$; see table 3). Specimens from Morocco tended to capture the largest proportion of bigger prey (i.e. *Rattus*), and a lower proportion of the smallest ones (i.e. geckos and small saurians).

There were ontogenetic dietary changes in terms of frequency of prey consumed: group I (255 < SVL < 600 mm) differed from group II (600 mm < SVL < 800 mm) and group

Table 3. Comparative data on body size, diet and reproductive ecology for populations of *C. hippocrepis* separated by the Strait of Gibraltar.

	Rif population (South of the Strait)	Baetic population (North of the Strait)
Source	actual study	Pleguezuelos and Moreno (1990), Feriche (1998), Pleguezuelos and Feriche (1999)
mean SVL (mm)	712.3 ($n = 141$)	685.6 ($n = 247$)
sex-ratio (males : females)	1.12 : 1	1.03 : 1
frequency of main prey groups in the diet	mammals (45%) reptiles (28%) birds (17%) amphibians (10%)	mammals (47%) reptiles (45%) birds (6%) invertebrates (2%)
mean prey size (SVL, mm)	77.7	52.5
size at sexual maturity (SVL, mm)	540 (males) / 720 (females)	500 (males) / 680 (females)
oviposition timing	end June / beginning July	end June / beginning July
clutch size: mean (range)	6.1 (3-10)	6.8 (3-10)

III (SVL > 800 mm; G-test, df = 1, $P < 0.02$ in both comparisons), but no difference was detected between Group II and III (table 2). In particular, the importance of endotherms increased with increases of snake body size, whereas the opposite was true for reptiles consumed. Group I did not prey on birds (table 2). There was a relationship between snake body size and prey size ($r = 0.56$, $n = 53$, $P < 0.001$; fig. 1A), but not between absolute body size of the snake and relative prey size (calculated as prey SVL/snake SVL, $r = -0.12, n = 53$, $P = 0.4$; fig. 1B).

There were intersexual differences in prey frequency (G-test = 28.3, df = 8, $P < 0.000$): females consumed more saurians and birds and fewer mammals, than males (table 1). No difference was detected in prey size (ANCOVA with SVL as covariate, $F_{1,52} = 0.18$, $P = 0.68$), prey mass (ANCOVA with SVL as covariate, $F_{1,52} = 1.51$, $P = 0.22$), or prey number in the gut of each specimen with prey (M-W U-test, $U = 245$, $P = 0.71$), the overlap between sexes in the trophic niche being moderately high ($\alpha_{jk} = 0.72$).

All prey had been swallowed head-first ($n = 24$).

Reproductive ecology

For reproductive data, 101 specimens (57 males, 44 females) were examined. In males, the RTV did not increase with body size in specimens with SVL < 540 mm, most of them having been collected in spring. Starting from that body size, there was a testicular recrudescence that represented a 10-to-14 fold increase of the RTV (fig. 2A). Therefore, males > 540 mm SVL were considered sexually mature, and males mature at about 40% of their maximum length (see results for body size in this sex). The smallest females with signs of reproductive activity had follicles between 8-17 mm in diameter, and a SVL of 720 mm; this was taken as the minimum size at which females attained sexual maturity. All the females with body size between 600-720 mm collected in spring had follicles under

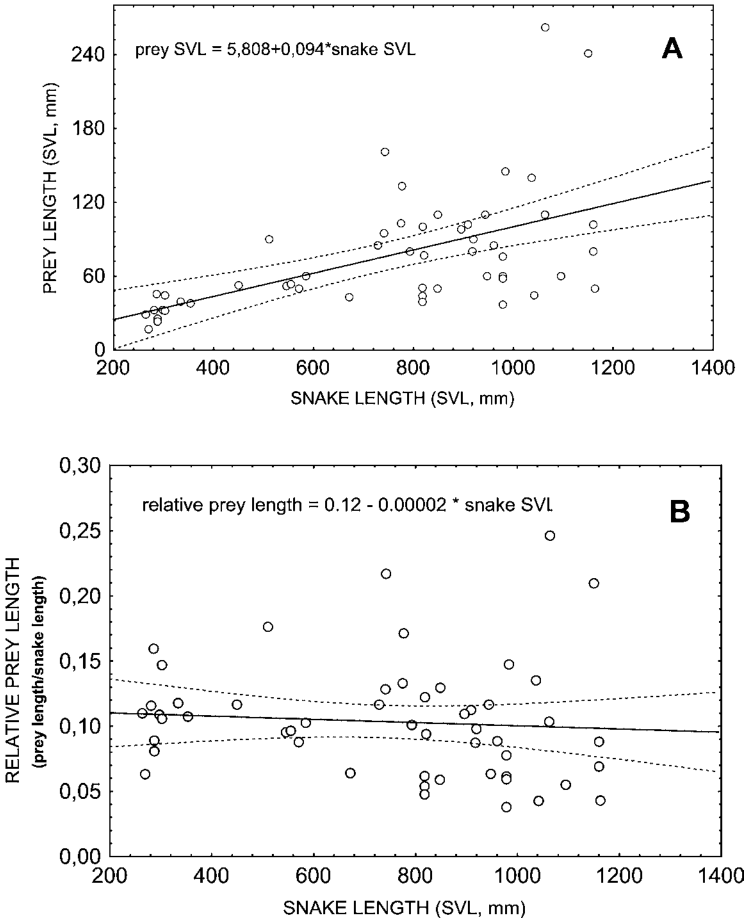

Figure 1. Prey size (A) and relative prey size (B) as a function of SVL in *C. hippocrepis* in the Rif region (northern Morocco). For more details, see the text.

8 mm in diameter (fig. 3A), which is the minimum size for vitellogenic follicles in this species (Pleguezuelos and Feriche, 1999). Therefore, in the Rif, females matured at about 55% of their maximum length (see results for body size in this sex).

For only adult males ($n = 34$), testicular recrudescence began in March, peaked in June, decreased in mid-July to a minimum volume, and remained so through fall and winter to the next spring (fig. 2B). The annual cycle of the RTV indicated that males have a vernal spermatogenesis cycle. Considering only adult females ($n = 17$), we observed that in the Rif the female reproductive cycle was seasonal (fig. 3B): vitellogenesis begun in May, and oviductal eggs were present from late May to late June. Four females from July (captured in 2nd, 12th, 18th, 22th) showed oviductal marks of recent oviposition (fig. 3B). Thus, oviposition was estimated to occur between the end of June and the beginning of

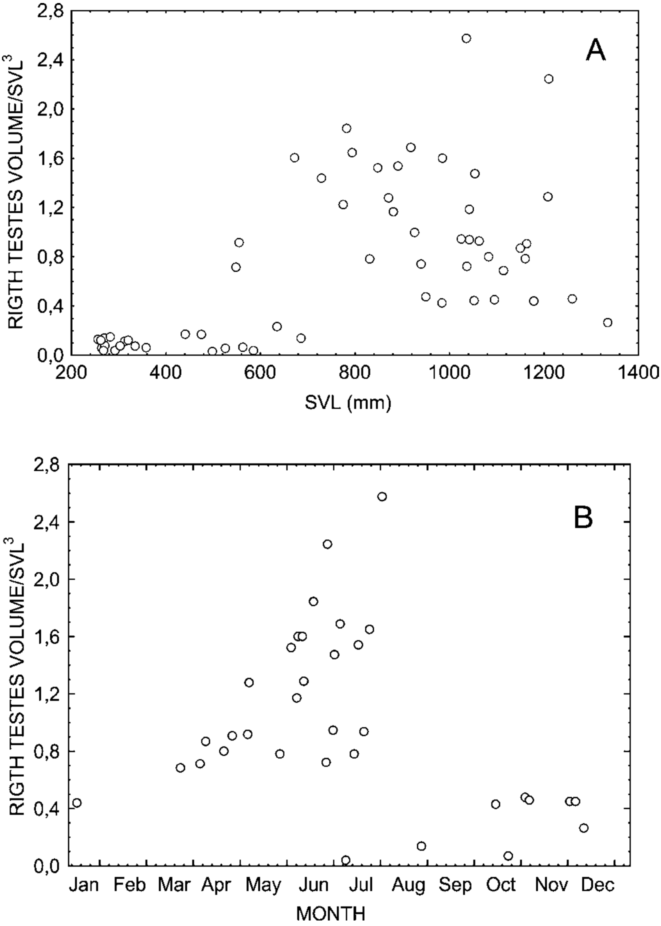

Figure 2. Relative testis volume in males of *C. hippocrepis*: (A) plotted against body size (SVL; all individuals; $n = 57$), and (B) plotted against month (only reproductive individuals, $n = 34$).

July. In females, abdominal fat bodies were large from March to middle May (before the vitellogenesis), and reached the lowest value in June and July (during vitellogenesis, see fig. 4). In mature males, abdominal fat bodies were roughly homogeneous throughout the year.

During May-July, 9 out of 12 females (78.6%) with SVL > 720 mm contained oviductal eggs or had recently oviposited. So, it is likely that adult females have annual reproductive cycles. Among the three non-reproductive females, two were close to the smallest size to be considered sexually mature (SVL, 724 mm and 755 mm). This suggests that 720 mm SVL is only a rough approximation of size at sexual maturity, and it is likely that some females may be reproductive for the first time with a size larger that this threshold value.

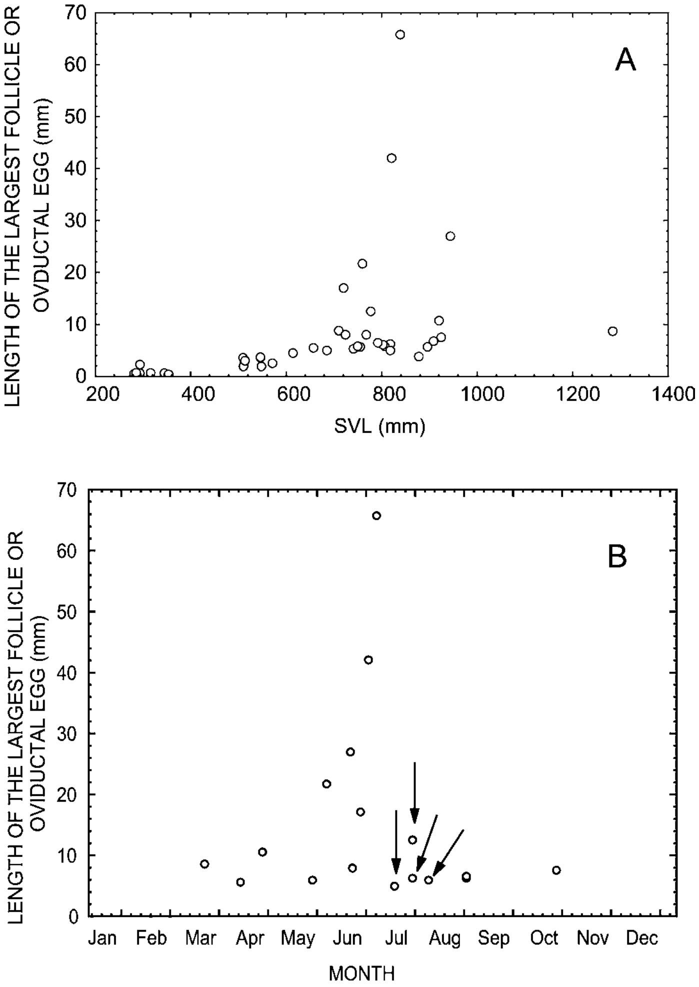

Figure 3. Length of the largest follicle and oviductal egg in females of *C. hippocrepis*: (A) plotted against body size (SVL; all individuals; $n = 44$), and (B) plotted against month of the year (only reproductive females, SVL > 720 mm; $n = 17$). Arrows indicate females with signs of recent oviposition.

Clutch size ranged 3-10 ($\bar{x} = 6.1 \pm 2.8$, $n = 9$). There was no significant relationship between maternal SVL and clutch size ($r = 0.45$, $n = 9$, $P < 0.22$; fig. 5).

Offsprings were observed in the wild during the first half of September; therefore, the egg incubation period was estimated to be approximately 60-70 days. Offsprings ranged 256-338 mm SVL ($\bar{x} = 287.5 \pm 24.3$ mm, $n = 10$), and weighed 6.0-9.0 gr ($\bar{x} = 7.8 \pm 1.0$ gr, $n = 9$).

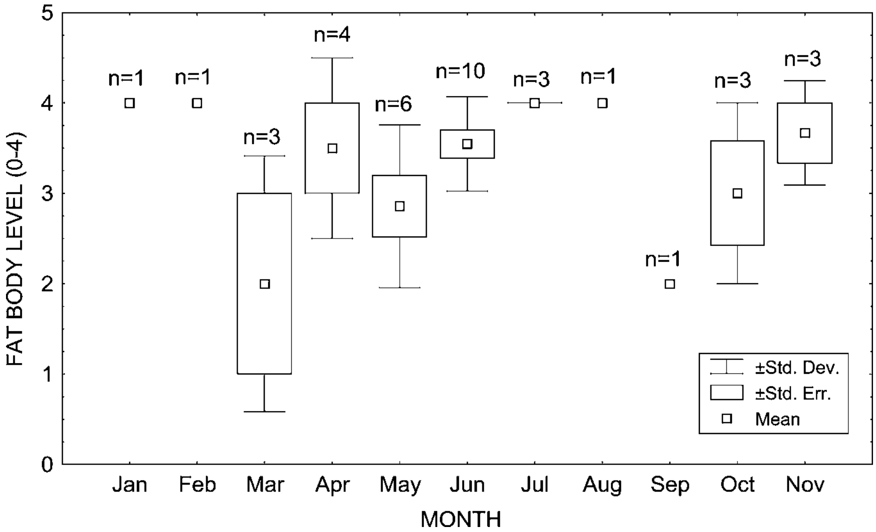

Figure 4. Abdominal fat level for reproductive females of *C. hippocrepis*. Fat body level was scored in five categories, from zero to four; more details are in the text.

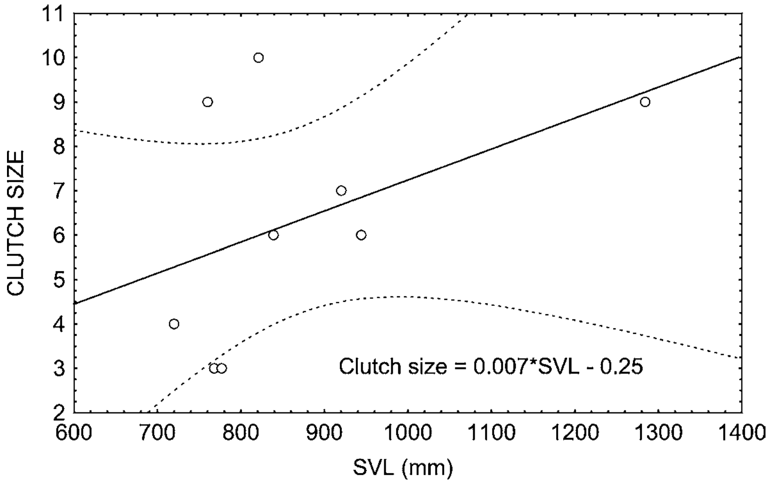

Figure 5. Relationship between maternal body size (SVL) and number of eggs in females of *C. hippocrepis* ($n = 9$).

Discussion

The first finding in our study is that populations of the Horseshoe Whip Snake separated by the Strait of Gibraltar are quite similar in body size, sexual size dimorphism, and sex ratio (table 3). Previously we demonstrated that another colubrid species (*Macroprotodon* *cucullatus*) with populations separated by the Mediterranean Sea and under different environmental conditions, underwent a shift in body size over a short geological time (Pleguezuelos et al., 1994). Variation in body size between conspecific populations geographically separated may arise when these populations are under different climate, interspecific competition, food resources, predation intensity, etc. (Dunhan et al., 1978). Thus, we suggest that the various populations of *C. hippocrepis* considered here, should be approximately under the same selective pressures on both sides of the Strait of Gibraltar.

Coluber hippocrepis showed, in the Rif, a diet similar to that of conspecifics from elsewhere (Vericad and Escarré, 1976; Meijide and Salas, 1987; Pleguezuelos and Moreno, 1990; Capula et al., 1997; Corti et al., 2000). Indeed, it is a generalist that preys on rodents, lizards, birds and amphibians. However, the Rif population preyed frequently upon amphibians, which are not consumed by other conspecifics from northern Mediterranean areas. The frequency of occurrence and the constancy of the presence of amphibians in the diet of the Rif population is significant enough to conclude that batracophagy is not an opportunist feeding event by a few specimens. The Rif population also consumed many more large micromammals and birds, and far fewer small saurian and small micromammals than did the Baetic population (Pleguezuelos and Moreno, 1990). The differences are more striking when a superficial comparison in prey availability is performed: species-richness in amphibians, and even abundance, is low in the Rif compared with the Baetic region (6 versus 12 species), the opposite being true for small saurians (23 versus 10 species; unpublished data of the authors). Therefore, the difference in the use of such a prey type is unlikely to be simply a consequence of prey availability. Genetic differences in prey preferences have been suggested for geographically separated conspecific snake populations (Arnold, 1992), and the evolutionary diversification of snakes seems to be closely related to the evolution of their feeding habits (De Queiroz et al., 2001). Birds as prey were mostly complete broods and fledged chicks of *Passer domesticus*, which indicates that the Horseshoe Whip Snake raids nests frequently. The high predation on large micromammals (rats), mirror results on the diet of this species in Pantelleria Island (Capula et al., 1997). However, it must be stressed that the two study areas are not comparable, as very specific life-history adaptative shifts of populations on islands are frequent (Schwaner, 1985; Capula et al., 1994). Moreover, in Pantelleria the Horseshoe Whip Snake has a very unusual foraging mode, feeding frequently on carcasses of rats (Capula et al., 1997). As a consequence of the differences in prey types, there were also remarkable differences in prey size: Rif snakes preyed on larger items as compared to those of northern Mediterranean snakes (Pleguezuelos and Moreno, 1990).

The Rif population also preyed less frequently on rupicolous prey (*Tarentola*, *Podarcis*), in comparison to the Baetic population (19% versus 40%) although the snakes are also tied to rupicolous habitats in the Rif (Fahd, 2001), as it is elsewhere. However, in accordance with other studies, most of the prey consumed in the Rif were nocturnal (61.5%; *D. pictus*, *R. saharica*, *T. mauritanica*, *S. fasciatus*, *S. etruscus*, *O. cunniculus*, *L. barbarus*, *Rattus* sp., *Mus* sp., *A. sylvaticus*). As the Horseshoe Whip Snake is primarily diurnal (Pleguezuelos, 1997), we conclude that this species may forage actively, relying on olfactory and visual cues, seeking for the diurnal retreats of its nocturnal prey (pers. obs.), which is in accordance with the findings in the northern Mediterranean (Pleguezuelos and Moreno, 1990).

The positive relationship between predator and prey body size suggests that the ontogenetic shift in prey-type simply occurs as a consequence of a shift in predator gape size: the larger the predator gape size, the larger the prey that can be ingested. However, the coefficient of determination for the regression of prey length on snake length was rather low (adjusted $R^2 = 0.26$), that is, 74% of the variance in prey length was not explained by the variation in snake length. As consequence of the former, we failed to find a correlation between predator size and the relative size of its prey. That is, large snakes are able to ingest large and small prey, and in this population some large snakes ate very small prey. Thus, there is no ontogenetic shift in lower size limit (Arnold, 1993).

Males of the Horseshoe Whip Snake mature at a smaller absolute and relative size than do females, despite a sexual size dimorphism indicating larger eventual size of males. This pattern seems to be the rule in Mediterranean colubrids (Feriche, 1998), and the delay in maturity for females may be a consequence of fecundity in that gender being a function of body size (Schwaner and Sarre, 1988).

The reproductive cycle is seasonal, with a single reproductive period each year in both sexes, as is known for all Mediterranean snakes (see review in Böhme, 1993, 1999). Our data on the spermatogenic cycle of males confirm previous data for the same species in both Morocco (Saint Girons, 1982) and the Iberian Peninsula (Pleguezuelos and Feriche, 1999). The spermatogenesis is prenuptial, occurs in spring, and implies a delay in the mating period. Although we lack direct observations of mating for the Rif population, this event occurs for the Iberian and the Pantelleria populations in the second half of May (Cattaneo, 1985; Pleguezuelos and Feriche, 1999), approximately three months after emerging from hibernation. Mediterranean colubrids with a different spermatogenetic cycle (aestival) normally mate shortly after emerging from hibernation (Feriche, 1998). Until now, the prenuptial spermatogenesis of the Horseshoe Whip Snake is only shared in Western Palearctic probably with *Coluber algirus* and certainly with *Malpolon monspessulanus* (Feriche, 1998). This characteristic enables snakes to complete their reproductive cycle (from spermatogenesis of males to hatching of newborns) in a single calendar year, as opposed to the aestival cycle, which requires two calendar years to complete an entire reproductive cycle (Saint-Girons, 1982).

Given that spring mating is delayed, consequently the female reproductive cycle is delayed, as observed in both the Baetic and the Moroccan population (Pleguezuelos and Feriche, 1999). Apparently, females carry vitellogenic follicles and oviductal eggs for only a brief period of time, approximately two months. For the Baetic population, we assumed that this short period of time carrying eggs was because females seek to lay as soon as possible, to avoid the unfavourable high temperatures of mid summer (Pleguezuelos and

Feriche, 1999). In this southernmost study area, where summer temperatures are even higher, this interpretation gathers more strength.

Fat-body cycles in females of the Horseshoe Whip Snake are closely linked to the reproductive cycle: vitellogenesis was associated with an apparent decline in the fat-body levels, suggesting that stored lipids contributed to the energy needed for follicular maturation and egg yolking, as reported in other Temperate Zone species (Bonnet and Naulleau, 1995; Santos and Llorente, 2004).

Several other traits of the reproductive ecology of *C. hippocrepis* (i.e. body size at sexual maturity, timing of the reproductive cycle in both males and females, fecundity, frequency of reproduction, hatching time, body size of newborns), appeared strikingly similar between the conspecific populations separated by the Strait of Gibraltar (see Feriche, 1998; Pleguezuelos and Feriche, 1999; table 3). The only observed difference, i.e. the lack of correlation between maternal body length and clutch size in the Rif population, is likely simply an artefact of the small sample size.

Data reported here on the natural history of a colubrid snake in the geographical area where the species originated, if contrasted to similar data from another population separated from the former for presumably 5.3 millions of years (Maldonado, 1989), led us to conclude that some natural-history traits (e.g., reproductive aspects), are likely evolutionary conservative. Body-size traits also remain similar between populations, although there are many divergent examples in snake populations separated by geographical barriers (Schwaner, 1985; Pleguezuelos et al., 1994; Tanaka and Ota, 2002). The trait which apparently diverged more between the two populations was the feeding ecology, as there were differences in the prey category consumed, prey size, and, to a lesser extension, in the ecology of the prey consumed. In generalist snakes such as the Horseshoe Whip Snake, diet habits should be the most plastic trait of its ecology, as has been established for many other colubrid species (Schwaner, 1985; King, 1993; Daltry et al., 1998). The ecological diversity of the diet was higher in the Rif population ($H' = 2.54$) than in the Baetic one ($H' = 1.91$; computed from the data of Pleguezuelos and Moreno, 1990), although the sample size differed by as much as 1.52-fold in favour of the Baetic population (sample size, 214 versus 141). We suggest that the Horseshoe Whip Snake may be more fitted to its prey in the geographical area where the species evolved, which is North Africa and nor Europe.

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