Geographic variation in reproductive output of female European whip snakes (*Hierophis viridiflavus*)

Marco A.L. Zuffi[1], Sara Fornasiero[1] & Xavier Bonnet[2]

[1]*Museum of Natural History and Territory, University of Pisa, Italy*

[2]*CNRS, CEBC, Centre d'Etude Biologiques de Chizé, Villier en Bois, France*

In snakes, body size and reproductive output vary greatly among disjunct populations. Clutch size is notably influenced by food availability, thermal conditions and maternal body size. A comparison between three large-scale areas – north continental, south continental and island populations of European whip snakes – revealed significant variation in body size and reproductive output. More importantly, there was a geographical difference in the covariation between clutch size and maternal body size, two traits mechanistically linked as body size constrains clutch size. This suggests that clutch size can vary independently of maternal body size, a situation that provides opportunities to tease apart the contribution of phenotypic plasticity from local genetic adaptations in these two life-history traits.

Key words: clutch size, islands, life-history traits, maternal body size

INTRODUCTION

Many organisms display significant phenotypic variation in response to various environmental conditions. As a result, populations are often characterized by a particular set of traits (e.g. coloration, body size) over their distribution range. Abundant field and experimental studies have demonstrated that body size, body shape, reproductive output and behaviour, for instance, show large variations in response to changing conditions such as thermal conditions or prey availability (Dobson & Murie, 1987; Gregory & Larsen, 1993; Reznick & Yang, 1993; Rohr, 1997; Bonnet et al., 2001a,b, 2003; Boback, 2003; Morrison & Hero, 2003; Mikolajewski et al., 2005). This regional variation can be an adaptation to local conditions associated with genetic differentiation (Madsen & Shine, 1993; Bronikowski, 2000; Pearson et al., 2002); however, phenotypic variation can be expressed independently of genotypic variation (i.e. phenotypic plasticity; Ford & Seigel, 1989; Madsen & Shine, 1993; Pigliucci, 2001; Zuffi, 2001; Mesquita & Colli, 2003; Aubret et al., 2004). Thus, to correctly describe the characteristics of a given species, and to determine its capacity to cope with environmental fluctuations (e.g. modification of the habitat, climatic change), it is necessary to collect basic information on variables such as body size and reproductive parameters over a wide variety of environmental or geographical situations. Unfortunately this information is lacking for the vast majority of organisms.

Reptiles are no exception to the scarcity of field information documenting the possible range of geographical variation. This is particularly true for snakes. Currently, despite the limited number of species, there is a lack of data relating to phenotypic plasticity and geographical variation of snake species, including the European whip snake (*Hierophis viridiflavus*), throughout Europe.

The aim of this study is to provide information on maternal body size and reproductive output of the European whip snake over a wide geographic range, from mid-western France to the south of Italy, including some island populations. Reproduction in female *Hierophis viridiflavus* appears to be one of the least studied aspects of this species' biology. Only a limited number of papers address reproductive traits, all of which consider single populations from limited areas (Bonnet & Naulleau, 1994; Capula & Luiselli, 1995; Capula et al., 1995; Luiselli, 1995). We are not aware of any single work on our study species dealing with comparative aspects of life-history traits throughout its distribution area. In this study we focused on two questions. Does maternal body size vary between populations inhabiting remote (e.g. islands versus mainland) and/or climatically divergent areas (northern versus southern Europe)? If so, does reproductive output vary accordingly? In snakes, as in other squamates, body size is largely influenced by local conditions and is linked to reproductive output (e.g. Seigel & Ford, 1991; Adolph & Porter, 1993; Shine & Seigel, 1996). Indeed, the positive influence of maternal body size on clutch size is well established in reptiles (e.g. Ford & Seigel, 1989; Shine et al., 1996; Bizerra et al., 2005). Inter-population comparisons may theoretically lead to two main situations. Female body size and fecundity (clutch size) may co-vary in a more or less parallel manner. Alternatively, we may observe a certain decoupling between these two traits. In other words, fecundity may be a simple consequence of changing maternal size; conversely, adaptation to local conditions (population genotypic characteristics) and/or phenotypic plasticity might produce different patterns in the relationship between female body size and fecundity, physiological regulations acting differentially on each trait. As a consequence, we may observe, for example, populations of small but highly fecund females versus populations of large females producing small clutches.

Table 1. Geographic source of the material examined.

Locality	Geographic area	Living (field)	Living (literature)	Preserved	Total
Chizé (France), Pamiers S. (Toulouse, France)	Mainland North	28		4	32
San Rossore, Arnino, Calci (Pisa, Italy)	Mainland South	0		2	2
Tolfa mountains (Rome, Italy)	Mainland South	0	13	0	13
Asinara (NW Sardinia, Italy)	Island	0		2	2
Capraia (Tuscan Archipelago, Italy)	Island	0		1	1
Gorgona (Tuscan Archipelago, Italy)	Island	0		1	1
Montecristo (Tuscan Archipelago, Italy)	Island	2		1	3
Pianosa (Tuscan Archipelago, Italy)	Island	0		1	1

We stress that the current study is preliminary; our goal was not to encompass the whole array of geographic variation but to describe the relevant aspects of this species' reproductive biology that are still lacking in the literature.

MATERIALS AND METHODS

The European whip snake *Hierophis viridiflavus* is a large (up to 200 cm total length; Bruno & Maugeri, 1990; Heimes, 1993) colubrid snake of the Mediterranean region. It ranges from western and north-eastern France to Switzerland and Italy, and also occurs on most of the western Mediterranean islands (Schätti & Vanni, 1986; Heimes, 1993). It inhabits a great variety of habitats, including lowlands and mountainous habitats up to 2000 m a.s.l., dry forests or wetlands (Bruno & Maugeri, 1990; Scali & Zuffi, 1994; Naulleau, 1997). Still common within its range, this species is sexually dimorphic with males attaining larger body size (Springolo & Scali, 1998), and exhibits two contrasting dorsal colour patterns (i.e. brownish-green and yellow versus black pattern; Heimes, 1993). Recent studies have documented the tendency towards larger body size in Italian continental populations compared to insular ones (Scali et al., 2003; Fornasiero, 2004), but none of these works explored the relationship between variation in mean body size and reproductive output. The reason for the scarcity of detailed information on reproductive traits of this species is the low occurrence of female specimens in both herpetological collections and in the field (Capula et al., 1997, 2000; Bonnet et al., 1999). This is probably due to the high elusiveness and limited mobility (Ciofi & Chelazzi, 1994) of females.

We examined 55 reproductive females (both living and museum-preserved specimens) originating from northwestern France, central Italy and small islands (less than 50 km^2) in the Tyrrhenian Sea (Table 1). Thirty living animals provided original field data, information on 13 other females was obtained from the literature (Capula & Luiselli, 1995) and other data were collected from 12 museum specimens. We decided to include data from published papers and from museum specimens in our analysis because, due to the scarcity of information on the reproductive biology of this species, we believe that a large-scale comparison of life-history traits is of primary importance. In our sample (both living and preserved specimens) we measured snout–vent length (SVL) and total length (TL, only with intact tail) to the nearest 0.5 cm. Only TL and clutch size were available for literature specimens. In our sample, clutch size was measured using two methods. Firstly, for those free-ranging females close to deposition (1–6 days before laying eggs, as detected by manual inspection), females were caught by hand, returned to the laboratory and kept in individual cages until eggs were laid. Following egg laying, females were released at their site of capture; similarly, neonates were released after hatching. When females were not close to deposition, but had detectable and well-developed, oviductal eggs (more than 30 mm long), we determined clutch size from palpation and released them immediately to avoid egg reabsorption as a consequence of captivity stress. Secondly, museum specimens were dissected and the total number of well-developed, oviductal eggs counted (follicular eggs were not considered). In this species the females do not lay more than one clutch per year, and therefore we used clutch size as an index of annual fecundity. It was not possible to determine reproductive parameters such as relative clutch mass, firstly because some of our specimens were of museum origin, obviating any estimation of clutch mass, as well as offspring and female body mass; secondly, as previously stated, not all the living females were kept until they laid eggs; and finally, no information about female body mass and clutch mass was available from the literature.

The sample was subdivided into three groups corresponding to three disjunct geographic areas: north mainland (France, Deux-Sèvres department, in the vicinity of the CEBC–CNRS, 46°07'N, 00°25'W); south mainland (central Italy, specimens from Tuscany and Latium); and islands (Tuscan Archipelago from about 43°30'N, 10°00'E to 42°10'N, 11°10'E, and Asinara island, 41°04'N, 8°16'E). This subdivision was made in order to separate different climatic conditions (Deux-Sèvres district is characterized by a humid oceanic climate, while central Italy and the Tyrrhenian islands are characterized by a Mediterranean, dry climate) and geographical features (mainland versus small islands with a long isolation period, e.g. more than 15,000 years). Because data from the literature did not include measures for all the variables of interest (e.g. SVL), we used the linear regression of SVL on TL from our field and museum data to infer SVL. The regression equations did not differ significantly between the geographical areas considered (ANCOVA, SVL as the dependent
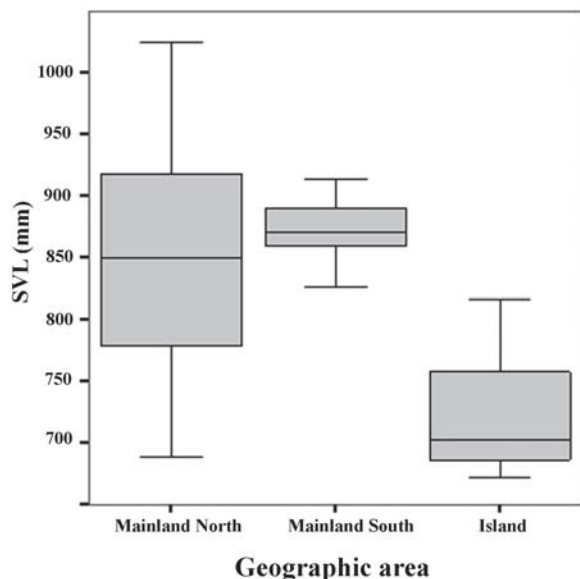
Fig. 1. Geographic variation in mean body size (median, interquartile range and extremes) of reproductive female *Hierophis viridiflavus*.

variable, TL as the covariate, geographic area as factor, $F_{2,40}=0.02$, $P=0.998$; homogeneity of slopes assumption was met). Original versus inferred variable values were highly correlated (Pearson correlation=0.983, $P=0.0001$, $n=44$). Within each of the three main groups of females, maternal body size and clutch size distributions did not deviate from normality (all Kolmogorov–Smirnov Z tests led to P values greater than 0.05, ranging from 0.25 to 1.00). Individuals kept in alcohol are not likely to increase in size or to shrink by more than few centimetres (if at all) (Reed, 2001), whilst clutch size is unaffected: considering living versus preserved specimens did not change any results (all interaction terms between biometrical and reproductive features led to P values greater than 0.1); therefore we pooled these two categories of animals in subsequent analyses. In analyses in which assumptions for parametric statistics were not met (e.g. homogeneity of variance), we used non-parametric tests (Kruskal–Wallis test, followed by non-parametric Dunn multiple comparison test). Statistics were performed using Statistica 6.1 and SPSS 8.0 and 12.0 programs.

RESULTS

Maternal body size

We found significant variation in snout–vent length between geographic regions (Kruskal–Wallis, with geographic area as the factor and maternal SVL as the dependent variable; $H=16.002$, $P<0.001$, $n=55$, Fig. 1). A post-hoc Dunn multiple comparison test indicated that mainland snakes attained similar body sizes ($Q=1.063$, NS) and that island snakes were significantly smaller ($Q=3.463$, $P<0.002$ and $Q=3.883$, $P<0.001$ with respect to mainland north and mainland south animals).

Clutch size

Clutch size showed strong geographic variation (Kruskal–Wallis test with geographic area as the factor and clutch size as the dependent variable; $H=31.755$, $P<0.0001$, $n=55$, Fig. 2). A post-hoc Dunn multiple comparison test revealed that the north mainland females produced significantly larger clutches than south mainland and island snakes ($Q=4.92$, $P<0.001$ and $Q=3.798$, $P<0.001$ respectively) (Fig. 2). No differences were found between island and south mainland clutch sizes ($Q=0.094$, NS). Maternal body size positively influenced clutch size overall ($r=0.222$, $F_{1,53}=1.435$, $P<0.001$, Fig. 3). Therefore, we took this relationship into account in examining geographical variation in clutch size. A Kruskal–Wallis test performed on standardized residuals calculated from linear regression of clutch size and maternal SVL for geographic areas suggested that maternal-size-adjusted clutch size varied among the three geographic areas ($H=32.834$, $P<0.001$, $n=55$, Fig. 4). A post-hoc Dunn multiple comparison test showed that the south mainland population's adjusted clutch size was significantly smaller than those of the other two (island: $Q=2.469$, $P<0.05$; north mainland: $Q=5.71$, $P<0.001$), while maternal-size-adjusted clutch sizes of north mainland and island snakes were not significantly different ($Q=1.79$, $P=$NS).

DISCUSSION

Our results clearly show that female European whip snakes exhibit significant phenotypic variations between disjunct geographic areas for at least two major life-history traits: body size and clutch size.

Our analyses revealed that maternal body size and clutch size, two mechanistically linked traits (Ford &
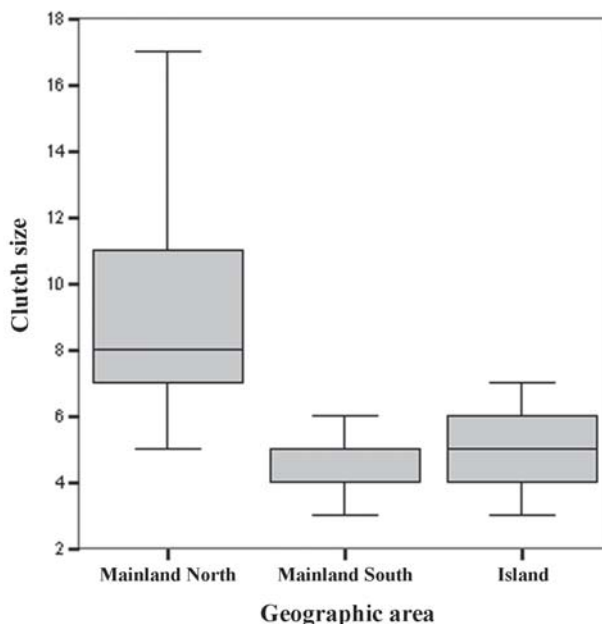

Fig. 2. Geographic variation in clutch size (median, interquartile range and extremes) of reproductive female *Hierophis viridiflavus* (original data).
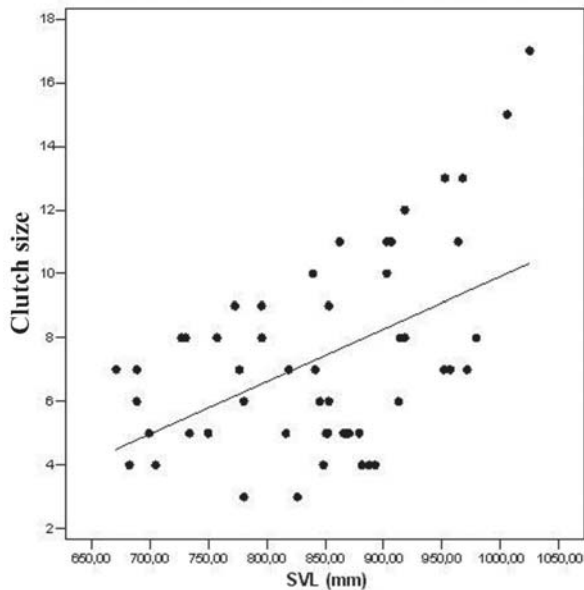
Fig. 3. Body size and reproductive output in female *Hierophis viridiflavus*.

Seigel, 1989; Shine et al., 1996; Bizerra et al., 2005), could vary with a certain degree of independence. Although our island sample mixed several localities, the small body sizes observed on the islands were both highly consistent and significantly distinguishable (all the females originating from any island were small), suggesting a general trend towards smaller island snakes. Clutch sizes were smaller in the southern mainland populations relative to the northern and island ones when maternal body size was taken into account. It should be noted that this latter result was relatively immune from potential artefacts arising from our methodology that mixed living (including literature) and museum specimens. Indeed, removing all the museum specimens did not change the results (comparison between southern and northern snakes: H=22.36, P<0.001, n=42), as expected from an inspection of Figure 4. Overall, sampling problems alone could not cause the geographic variations we reported, but instead they show that remote populations differ significantly for at least two major life-history traits. The fact that variation in clutch size was not simply a consequence of variation in maternal body size was also clearly revealed by the analysis of the residuals from the regression between maternal size and clutch size. The latter result is particularly important. Indeed, it suggests that despite the fact that maternal body size constrains clutch size, the regulations that act on each of these traits are relatively independent.

Nagy et al. (2003) showed that genetic differences exist to a certain degree among mainland northern and mainland southern snakes. This could be a possible cause for the observed differences in reproductive output between the two distinct groups, despite the absence of differences in maternal body size. However, in the absence of strong experimental data we cannot analyse the factors (genetic adaptation versus plasticity) that underlie the phenotypic divergences reported above; a correlational approach remains possible, however. Climatic factors and

food availability are two major sources that influence reptile size and reproduction. Several field and experimental studies have demonstrated that food intake, prey spectrum and prey quality can strongly influence body size, body shape and reproductive output in snakes (Madsen & Shine, 1993; Rugiero & Luiselli, 1995; Bonnet et al., 2001a,b; Zuffi, 2001). Similarly, ambient temperatures strongly influence all the above traits (e.g. Adolph & Porter, 1993; Lourdais et al., 2002). For example, among snake species, maturation of gonads in both sexes seems to be a process related more to body size and growth rate than to a fixed individual maturation age (e.g. Ford & Seigel, 1994; Madsen & Shine, 1994). It is also known that ectotherms with longer activity seasons (e.g. populations inhabiting regions with warmer climates) grow faster and therefore reach reproductive maturity at a younger age (Adolph & Porter, 1993 and refs therein). The attainment of sexual maturity slows down growth rate in reptiles (Andrews, 1982; Lagarde et al., 2001). Growth rates depend largely on food intake and ambient temperature for digestion. Therefore, it was of interest to explore if marked distinctive climatic and feeding regimes exist among the remote snake populations we studied.

Both climatic and food resources are very different among the areas studied: the respective climatic peculiarities of the northern (wet Oceanic climate) and southern (dry Mediterranean climate) areas under focus are well documented. Smaller females inhabit small Mediterranean islands (see also Fornasiero, 2004). Preliminary data suggest that island snakes follow different growth trajectories than mainland snakes, and therefore could be restricted to smaller average body sizes (S. Fornasiero, unpublished). Food availability is also deeply divergent among the areas. The small females from the small Mediterranean islands feed mostly on small prey: lizards
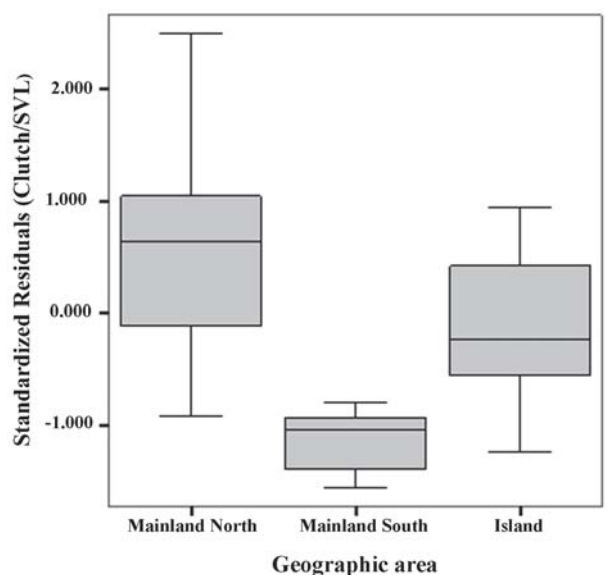

Fig. 4. Geographic variation in fecundity (median, interquartile range and extremes) in reproductive female *Hierophis viridiflavus* (standardized residuals clutch size/SVL).

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(Heimes, 1993) or amphibians (Zuffi, 2001; Zuffi & Picchiotti, 2005; M.A.L. Zuffi, unpublished data from preliminary analyses). This is not surprising as these islands, isolated from the mainland for a long time (in the case of our small Tyrrhenian islands, more than 15,000 years), host prey types of smaller size compared to those found on the mainland. It could be easier for snakes to retain a small body size to consume small prey on islands (Boback, 2003 and refs therein). Larger females were found in continental Italy or France; in these areas, the snakes feed essentially on relatively large prey: rodents, passerine birds and lizards of various sizes (Rugiero & Luiselli, 1995; Capula et al., 1997; Zuffi & Picchiotti, 2005; Zuffi et al., 2006).

It should be stressed that food availability and climatic conditions interact in complex ways. Annual variation in length of activity season (hence, the total number of prey eaten per year, and thus total annual prey mass) and the effective amount of energy gained after digestion could lead to different energy inputs, growth rate, maturation patterns and reproductive output (Adolph & Porter, 1993; Lourdais et al., 2002). Consequently, further studies of geographic variation in body size and clutch size in the European whip snake will need to gather both genetic and experimental data.

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