

Reproductive ecology of the slow worm (*Anguis fragilis*) in the northwest Iberian Peninsula

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Abstract—The reproductive characteristics of the slow worm (*Anguis fragilis*) were studied in A Coruña (Galicia, NW Spain) in 1999, 2000, 2001 and 2002. Data were mainly obtained through pregnant females captured in natural populations which subsequently gave birth under controlled conditions in the laboratory and the resulting neonates were examined. Marked individuals in a field population were also monitored. This field study allowed us to gain knowledge of the activity and reproductive cycle of the monitored population. A total of 68 births and 468 neonates were obtained, allowing us to determine the basic reproductive characteristics of the populations studied such as the litter size, offspring weight, offspring size and minimum maturity size for females: 135-150 mm snout vent length (SVL). The relationship between several variables related to offspring and their mothers showed a positive relation between size and mass of the litter and offspring with maternal size. A relationship between maternal tail length and litter mass was not observed. Unlike other studied populations of this species, most of the females of the A Coruña population (88.8%) reproduce annually. We found a probable relationship between female annual reproductive output and latitude, likely related to differences in environmental temperature. The activity cycle for the monitored population (from February to mid-December) is the longest known for the species.

Keywords: *Anguis fragilis*; life history; lizards; reproduction; slow worm; viviparism.

INTRODUCTION

The slow worm (*Anguis fragilis*) is a live-bearing lizard (Rollinat, 1934; Dely, 1981), with a wide distribution range over the western Palearctic (Cabela, 1997) which, on the Iberian Peninsula, is restricted to the Cantabrian-Pyrenean band and the mountainous areas of its northern half (Barbadillo and Sánchez-Herráiz, 1997; Salvador, 1998; Galán, 2002). Regardless of its wide distribution, studies on the biology of this species are still scarce, probably because of the difficulty

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entailed in marking and monitoring individuals (Gregory, 1980; Stumpel, 1985; Smith, 1990; Platenberg, 1999). There are several works that report on reproductive biology in populations from western and central Europe (Patterson, 1983; Smith, 1990; Platenberg, 1999; Beebee and Griffiths, 2000) and high altitude populations in the Alps (Capula *et al.*, 1992; Capula and Luiselli, 1993). On the Iberian Peninsula data on the reproduction of this species are very limited. Only Braña (1983) gives some information on the reproductive characteristics of the slow worm in Asturias (northern Spain), and diverse information is also included in general studies on Iberian herpetofauna (Salvador, 1998; Barbadillo *et al.*, 1999; Salvador and Pleguezuelos, 2002). With regard to Galician populations, only fragmentary information has been published in papers of a general nature (Galán and Fernández Arias, 1993; Galán, 1999).

The main objective of this study is to provide information on some basic aspects of the reproductive ecology of the northwest Iberian populations of the slow worm. The information obtained will be compared with data from different geographical areas. The results will be analysed in an attempt to understand the changes that affect the reproductive strategies of a taxon as an adaptive response to temperature conditions.

MATERIALS AND METHODS

This study is based on the results of two different methodologies. First of all, by obtaining births under controlled conditions we were able to have access to most of the information on the basic reproductive variables and the relationship between them. Secondly, a field study allowed us to gain knowledge of the activity and reproductive cycles of one population.

Reproductive characteristics

Females that gave birth in the laboratory were captured in natural populations from three low altitude locations in A Coruña province (NW Spain) during four study periods: from July to September in 1999, 2000, 2001 and 2002. Geographical data and basic climatic characteristics of these locations are summarised in table 1. In the reproductive period several weekly sampling visits (each 3-4 days) were made to these populations. On each visit individuals were captured by hand in their shelters, usually under stones, pieces of wood or other objects. After being captured, the individuals were sexed by their coloration and dorsal pattern, head shape and general body constitution (Stumpel, 1985; Smith, 1990). Females were examined to evaluate their reproductive condition. This examination was based on the detection of recent copulation marks, consisting of scale scratches on the head and neck caused by the biting of males during copulation (Rollinat, 1934). This condition was also determined by the stage of abdominal distension and the presence of embryos in advanced developmental stages, by means of harmless

Table 1.

Climatic data of the study areas. Values of average accumulated annual precipitations in mm (Ann Prec), average annual temperature in °C (Ann T), average temperature of the coldest month (T cold m), average temperature of the warmest month (T warm m) and thermal range (T range) are indicated (Martinez Cortizas et al., 1999). The altitude of these three zones is below 50 m a.s.l.

Study area	Location	Ann Prec	Ann T	T cold m	T warm m	T range
A Coruña	43°22'N, 8°24'W	906	14.1	10.2	18.9	8.7
Eume	43°24'N, 8°6'W	1383	14.3	7.9	19.6	11.7
Louro-Lariño	42°47'N, 9°5'W	1355	14.2	8.0	21.3	13.3

ventral palpation. The number of pregnant and non-pregnant females captured in each study period was recorded. Non-pregnant females and females in early stages of pregnancy were marked and immediately released at the capture point. Females in an advanced stage of pregnancy were taken to the laboratory, where their weight was recorded. Until they gave birth they were kept in captivity, isolated in individual plastic boxes measuring 30 × 20 × 10 cm, with loose substratum (topsoil or moss), and given water and food (*Tenebrio molitor* larvae and slugs of the genus *Deroceras*) ad libitum (Smith, 1990). Recipients were kept at laboratory room temperature (20–25°C) and checked daily until the births took place. Within 12 h after birth, the weight of the female and each neonate was recorded with an electronic scale (Scaltec SBC 41) to the nearest 0.001 g, and the snout-vent length (SVL) and tail length (TL) were measured with a steel calliper to the nearest mm. The relative litter mass was determined as the quotient between total mass of the litter and mass of the female after the birth. The total number of neonates and the number of live neonates in each litter were counted. The coloration and pattern in the neonates as well as any deformity detected were also recorded. Adult females and their offspring were marked and released at the capture point of the former.

Data from the 4 years of study were considered together in the statistical analysis of the relationship among variables, because of the relatively scarce amount of data obtained on each reproductive period and the results of the homogeneity test (Kruskal-Wallis test).

Activity cycles

The monitored population is located in a 5 ha zone dedicated to farming, pasture and leisure activities, placed in a built-up area in the town of Visma, on the outskirts of A Coruña, NW Spain (43°22'N, 8°25'W; UTM: 29T NJ40), at an altitude of 50 m above sea level and approximately 1 km from the coast. The Wet Oceanic climate type in the study area (Carballeira et al., 1983) is characterised by mild temperatures and frequent rainfalls homogeneously distributed over the year. The low annual thermal amplitude (8.7°C) and the low evapotranspiration values cause a short winter frost period (less than 1 month or non-existent), and a summer drought of less than 2 months. The vegetation consists mainly of a meadow used for reaping

Table 2.

Growth data from the marked population (males and females altogether), calendar year (CY), age in years, average growth rate in mm/day (GR), snout-vent length at the beginning of the growth period in mm (SVLb), snout-vent length at the end of the growth period in mm (SVLe), and number of recapture data used on each age class (N).

CY	Age	GR	SVLb	SVLe	N
1-2	0-1	0.157	48.72	98.80	19
3	1-2	0.137	98.80	136.50	11
4	2-3	0.049	136.50	150.02	7

and pasture for a small number of bovines, and is made up of several species of herbaceous plants (*Oenanthe crocata*, *Anthoxantum odoratum*, *Lolium multiflorum*, *Dactylis glomerata*, *Plantago lanceolata*, *Trifolium repens*, etc.). Bordering this zone there are small bush areas of *Ulex europaeus* and *Rubus* sp. and scattered woodland (*Alnus glutinosa* and *Salix atrocinerea*), as well as several vegetable gardens. This area is located about 100 m from the city limits of A Coruña and is next to a state school, so human presence in the area is high. The density of the monitored population was estimated by the Petersen method (Ferreiro and Galán, 2000).

Samples in this population were taken every 2 weeks all the year round. Individuals were captured by hand, after being located in shelters, mainly under stones. After the animals were captured, they were sexed, marked and the snout vent length (SVL), tail length (TL) and weight were measured. Data on coloration and pattern were recorded. The reproductive stage of females was also recorded (see above). Recapture records in the field of marked individuals born in the laboratory allowed us to determine the average size for 1-year-old individuals (SVL = 98.8 mm). Individuals under this size were considered to be yearlings. Through mark and recapture methods we were able to determine the growth rate for the first 3 years of life. Annual growth rates for males and females altogether are shown in table 2. Individuals larger than 99 mm SVL and smaller than 130 mm SVL, in males, were considered subadults, based on secondary sexual characters (Ferreiro, 2004); females larger than 99 mm SVL and smaller than 135 mm SVL were considered subadults (see Results). Individuals over 130 mm SVL in males and 135 mm SVL in females were considered adults.

The marks were made using an ophtalmic cautery (FIAB F 7255). Punctual burns were made on the dorsal scales of individuals (Stumpel, 1985). This kind of mark does not cause injuries to animals because of the thickness of their skin which also has osteoderms. These characteristics also avoid other kinds of marks such as subcutaneous tattoos or scale notching. These marks allow us to recognise individuals on recapture. Each individual was released at the capture point within 24 h after being caught (except females in advanced stage of pregnancy that were moved to laboratory and released after the birth).

The particular behaviour of this species (presumed to have an important fossorial activity and low individual detectability) has prompted us to make some assumptions to describe its natural history. Since slow worms, in this population, were not observed to be out of their shelters at any time, we considered the presence of individuals in superficial shelters to be an indication of an activity period or momentary rest time, as *Anguis fragilis* is an animal exhibiting mainly fossorial and secretive activity (Rollinat, 1934; Gregory, 1980; Gasc and Gans, 1990) and because of observations of signs of activity in the shelters (e.g., regurgitation of recently consumed prey). When individuals did not appear in these shelters, they were considered to be in an inactivity period (e.g., during the coolest periods of winter individuals of the slow worm did not appear in these shelters).

Throughout the year, there are periods when individuals of a particular age and size category are more easily captured than others (Stumpel, 1985; Smith, 1990; Platenberg, 1999; this paper). This would imply that *Anguis fragilis* does not comply with the basic premise of mark and recapture methods (i.e., equal probability of capture for all individuals; Platenberg, 1999; this paper). This behaviour, linked to the difficulty of finding animals in sufficient numbers, makes it hard to conduct a demographic study of this species. Growth rate for the first 3 years was obtained through mark and recapture data.

Reproductive frequency

We were not able to find a permanent mark method for this species. The reproductive frequency was determined by an indirect way using the rate of pregnant and non pregnant females found in each reproductive period (Patterson, 1983).

Combining the average individual fecundity with the frequency of reproductive females during each reproductive period, a value was obtained which may be called the annual average individual fecundity (*Fi*). This value shows the contribution, expressed as the number of neonates, that one adult female will make, on average, to the population in each year.

Statistical analysis

The independence of the data was tested on the main variables obtained through laboratory births by the run test, using the median as a cut-off point. Homogeneity was tested with the Kruskal-Wallis test, using the year of capture as the group variable. Normality was tested with the Kolmogorov-Smirnov test. Regarding the variables tested, the data analysis was carried out using SPSS 11.0 software.

RESULTS

The density of the monitored population (Visma, A Coruña) was estimated at 1700 individuals per hectare.

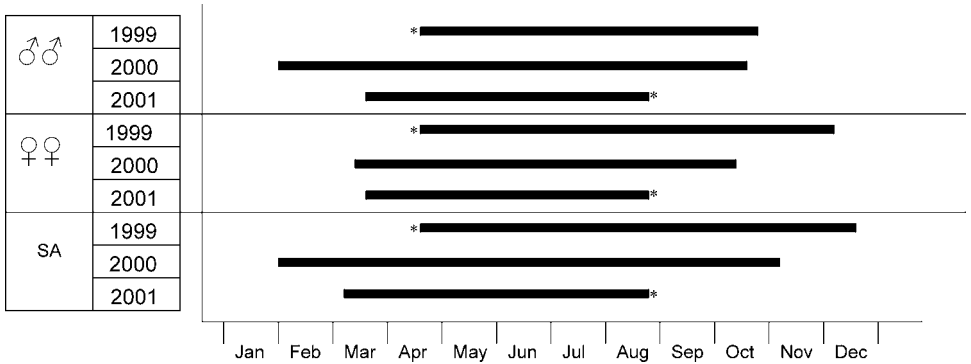


Figure 1. Activity periods for the different age and sex categories of *Anguis fragilis* in the study area of San Pedro de Visma (A Coruña) during 1999, 2000 and 2001. Each line represents the period in which individuals were observed that year. Asterisks show the beginning and end of sample periods for the years not including the whole activity period of the species. SA: subadults.

The number of births obtained during each reproductive period was not homogeneous throughout the study. There were variations, according to the following distribution: three births in 1999, seven births in 2000, 34 births in 2001 and 24 births in 2002. No differences in all the reproductive variables studied among the years (1999, 2000, 2001, 2002) were found (Kruskal-Wallis test, $P > 0.05$ in all cases). It was observed that the data did not differ significantly from a homogeneous and normal distribution of independent data.

Activity cycle

The population studied begins its activity in February-March, stopping in October-December. The activity period varies with the age and sex category of individuals, and an interannual variability was also found (figs. 1, 2). Adult males can be active from the beginning of February until mid-October, with a maximum activity period in March-June. Subadults are active from February until mid-December, with maximum values in May-June, while females are active from mid-March until mid-December, with a maximum in May-August (fig. 2). The sex ratio of the population, for the total number of individuals found, over the whole observation period, was 1.2 : 1 (males : females). In 2001 activity started later in males and subadults than in 2000, and in 1999 females and subadults extended their activity more than in 2000 (fig. 1).

Sexual maturity of females

The size of the smallest female observed in the field showing evidence of being pregnant, later confirmed with birth in laboratory, was 135 mm SVL. The next three pregnant females, in increasing size order, measured 141, 147 and 150 mm SVL. Thus, we consider the minimum maturity size of slow worm females in

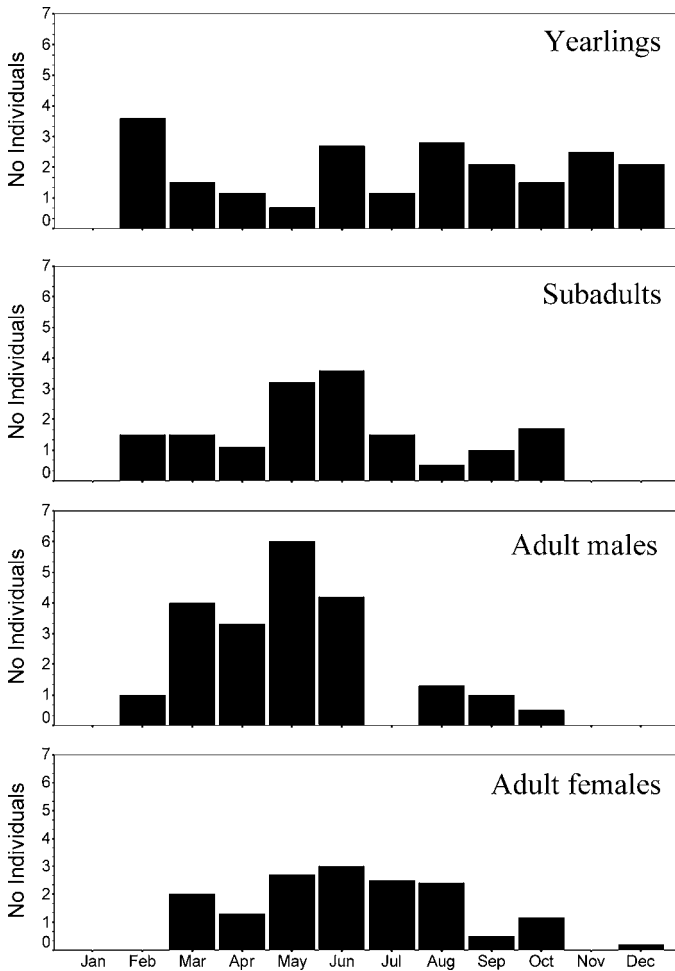


Figure 2. Number of captures by month. The average number of individuals, of each sex and size category, captured per visit on each month is given (No Individuals). Data from the San Pedro de Visma plot, years 1999-2001.

the population under study to be 135 mm with a possible variation range of 135-150 mm. Growth rates for the first 3 years (table 2) indicate that, on average, the adult size for females (135-150 mm of SVL) is reached between the end of its 2nd year of life, 3rd calendar year (CY) (average 136.5 mm) and the end of the 3rd year (average 150.0 mm), 4th CY. So the first reproductive event for a given female must occur in its 3rd year of life.

Reproductive cycle

Females showing recent mating scars were observed from the middle of March or April (first observations: 24/4/1999, 11/3/2000, 18/3/2001) until July (last observations 4/7/1999, 25/7/2000, 8/7/2001). Eighty percent of females showing

recent copulation scars were captured in the monitored population (Visma, A Coruña) between the beginning of April and the end of July ($n = 43$). We found that some females had very deep mating scars. It is likely that the mating scars may remain visible for some period of time after mating, so some of the scars observed, especially in July, could have been produced some time ago.

Females with embryos in advanced development stages (determined by abdominal distension and ventral palpation) appeared from late July or mid-August (10/8/1999, 17/8/2000, 29/7/2001, 21/7/2002) till middle-late September (10/9/1999, 12/9/2000, 22/9/2001, 18/9/2002). Considering the 4 years of observation together (1999, 2000, 2001 and 2002; 68 births), over 90% of births took place between 10 August and 15 September (91.2%). The first neonates appeared in the samplings taken from the monitored population in the middle of August (15/8/1999, 17/8/2000).

The total reproductive period (from the first mating event until the last birth) lasted, on average, from mid-March to mid-September, — a total of 152 days.

We found interannual variation in these cycles. The period of mating started earlier in 2000 and 2001 than in 1999. Nevertheless we did not find any appreciable differences in the climatic variables among the periods previous to matings (January-May) during these years (Instituto Nacional de Meteorología, 1999, 2000, 2001, 2002).

Reproductive characteristics

The main reproductive characteristics of females and offspring obtained in the laboratory during the 4 years of study are summarised in table 3. The great variability found among neonates is striking both in size and weight, even within the same litter. The most extreme case showed a litter of eight neonates, all of which were viable, with no observable deformation, where the largest one (0.770 g) weighed twice as much as the smallest one (0.332 g), and also had a different dorsal coloration. The standard deviation values for size (SVL) and weight in this litter were 4.166 and 0.158, respectively — greater than the ones corresponding to average size and weight variability among litters (3.16; 0.100; $n = 68$).

Of the neonates 97.1% ($n = 468$) were born alive and without observable deformation. Dead neonates were recorded for seven births (a total of 12 individuals). Two of the individuals born alive showed a visible deviation of the spinal column on the frontal plane (scoliosis) in the distal caudal region. Neonates could not be sexed because of the external similarity of both sexes until sexual maturity.

Most of the reproductive characteristics studied were related to female size (SVL): litter size ($r^2 = 0.294$; $F_{1,65} = 27.097$; $P < 0.001$, fig. 3), litter mass ($r^2 = 0.451$; $F_{1,65} = 53.383$; $P < 0.001$), average size of the newborn (SVL) ($r^2 = 0.273$; $F_{1,64} = 23.993$; $P < 0.001$, fig. 4) and average weight of the neonates ($r^2 = 0.223$; $F_{1,65} = 18.680$; $P < 0.001$). Other relations were found between litter mass and average mass of the neonates ($r^2 = 0.245$; $F_{1,65} = 21.360$; $P < 0.001$), as well as between litter size and offspring size ($r^2 = 0.813$; $F_{1,66} = 287.209$; $P < 0.001$). There was no relation found between female tail length and litter size

($F_{1,65} = 0.024$; $P = 0.877$). The relative litter mass, calculated as the quotient between litter mass and female mass after the birth is given in table 3. This value was not related to female size ($r^2 = 0.029$; $F_{1,66} = 1.962$; $P = 0.166$). The productivity of females, expressed as average number of young per mm of female SVL was 4.050×10^{-2} in 2001 ($n = 34$). In 2002 the figure was 4.053×10^{-2} ($n = 24$), and in 2000: 4.738×10^{-2} ($n = 7$).

The average relative litter mass was 0.282, with few variation among years (table 3).

Table 3.

Summary of the main variables obtained in the study of the reproduction along the years 1999, 2000, 2001 and 2002. For each variable, average with a standard error (SE), standard deviation (SD), minimum (min) and maximum (max) values and number of data (N) are shown.

Variable	average \pm SE	SD	min	max	N
Years 1999, 2000, 2001 and 2002 together					
Female SVL (mm)	168.30 \pm 2.15	17.81	135	208	68
Female weight (g)	13.762 \pm 0.51	4.261	6.938	28.659	68
Litter size	6.88 \pm 0.29	2.45	2	12	68
Litter size (viable neonates)	6.76 \pm 0.31	2.56	1	12	68
Litter weight (g)	3.817 \pm 0.19	1.608	1.114	8.311	68
Relative litter mass	0.282 \pm 0.01	0.095	0.09	0.53	68
Neonate weight (g)	0.549 \pm 0.006	0.100	0.276	0.798	468
Neonate SVL (mm)	48.72 \pm 0.14	3.16	40	56	468
2001					
Female SVL (mm)	171.38 \pm 2.79	16.24	147	208	34
Female weight (g)	13.627 \pm 0.66	6.306	7.210	24.047	34
Litter size	6.94 \pm 0.49	2.85	2	12	34
Litter size (viable neonates)	6.82 \pm 0.51	2.95	1	12	34
Litter weight (g)	3.939 \pm 0.32	1.870	1.114	8.311	34
Relative litter mass	0.290 \pm 0.02	0.116	0.09	0.53	34
Neonate weight (g)	0.554 \pm 0.006	0.104	0.276	0.798	237
Neonate SVL (mm)	49.10 \pm 0.22	3.32	40	55	237
2002					
Female SVL (mm)	162.42 \pm 3.42	16.73	135	196	24
Female weight (g)	13.074 \pm 0.80	3.943	6.938	20.235	24
Litter size	6.58 \pm 0.40	1.98	2	11	24
Litter size (viable neonates)	6.43 \pm 0.43	2.06	2	11	24
Litter weight (g)	3.609 \pm 0.26	1.287	1.211	6.452	24
Relative litter mass	0.2841 \pm 0.01	0.048	0.10	0.42	24
Neonate weight (g)	0.548 \pm 0.007	0.099	0.370	0.761	157
Neonate SVL (mm)	48.13 \pm 0.25	3.06	40	53	154

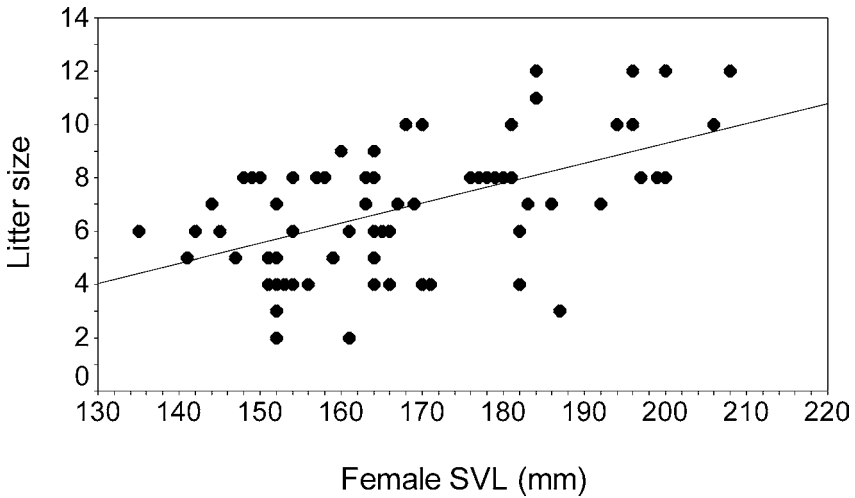


Figure 3. Relationship between litter size (total number of neonates of the litter) and snout-vent length of the female (mm).

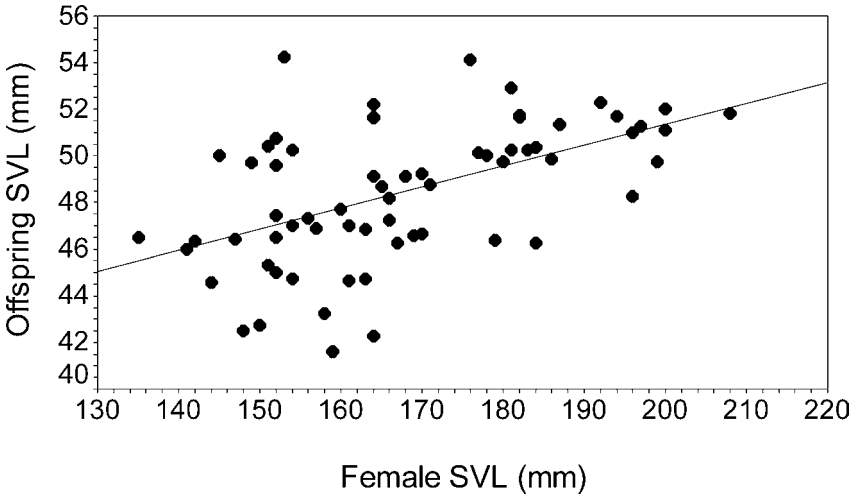


Figure 4. Relationship between offspring size: average snout-vent length (mm) of the neonates, and female snout-vent length (mm).

Reproductive frequency

During the field study it was not possible to determine the frequency with which reproduction took place in females using the mark and recapture methods because of the difficulties inherent to the study of this species, which give rise to a very low recapture rate (see above). There was only one instance recorded of a female that reproduced in 2 consecutive years. This female showed mating scars in March 1999 and June 2000, but not in March 2000 when it was also captured.

In 2000, 81% of the adult females captured in the reproductive period (April–July) showed evidence of pregnancy; were carrying developed embryos and/or subsequently gave birth in the laboratory ($n = 21$). In 2001, the figure was 92% ($n = 25$) and in 2002, 90% ($n = 52$). Most of the females in the populations under study (average 88.8% for the 3 years together, $n = 98$) reproduce yearly.

We observed interannual variation in the proportion of small reproductive females (SVL < 150 mm). In 2000 the proportion of small reproductive females was 14.3% ($n = 7$). In 2001, 2.9% of the total number of pregnant females that gave birth in captivity ($n = 34$) had a SVL below 150 mm. In 2002 the figure was 25% ($n = 24$). The average size of reproductive females varied from 171.4 mm in 2001 to 162.4 mm in 2002.

The F_i values for 2000–2002 are the following: $F_{i2000} = 6.02$; $F_{i2001} = 6.38$; $F_{i2002} = 5.92$; average F_i for the 3 years: 6.08.

DISCUSSION

Populations of the slow worm located in low altitude areas of the northwest Iberian peninsula may be considered as living in the most favourable climate for the species. Environmental conditions in this area are wet enough all year round so as not to require a summer rest period. In addition, they are warm enough to allow this species to be active for more than three quarters of the year, including a substantial part of the winter. This area is located in the Eurosiberian region, although it does have some Mediterranean climatic influence, making the winters not cold, but rather temperate. It is very important to take the latter into account to understand the natural history of the slow worm in these populations, particularly the timing of reproduction.

The climatic characteristics of the study area allow *Anguis fragilis* individuals to remain active from February to October or December. It constitutes the longest activity period registered for the species. A consequence of this long period of annual activity is an early onset of the breeding season and a long breeding season duration. The reproductive period begins, in the monitored population, in March–April, — earlier than in other populations studied (May–June in southern England; Smith, 1990; Platenberg, 1999), and lasts a total of 152 days, on average. In England, Smith (1990) reported a length of 85 days. Another important consequence of the long period of annual activity may be the capacity of a high percentage of females to reproduce annually. In other populations of slow worm, it has been reported that the majority of adult females do not produce young every year (Patterson, 1983; Stumpel, 1985; Smith, 1990; Capula et al., 1992). A biennial breeding cycle is the norm in Britain (Patterson, 1983; Smith, 1990; Platenberg, 1999). In the Netherlands, the percentage of pregnant females varied between 31 and 81% in different years (Stumpel, 1985). In Asturias, Braña (1983) reported a figure of 65% of pregnant females in the reproductive season. Reproductive frequency depends upon female size and environmental conditions. Smith (1990) suggested

the possibility of there being an increase in the frequency of reproduction in populations of southern Europe as compared to those of England, as was confirmed in this study. The lizard's capacity to produce litters (or clutches) depends on the amount of energy available for reproduction (Vitt and Cooper, 1985; Kozłowski, 1991; Doughty and Shine, 1997, 1998). The energy content of the carcass of slow worm females which are about to give birth is less than that of females that are not reproducing that year (Patterson, 1983). In the populations where *Anguis fragilis* reproduces biennially, it is probably that the shorter activity season gives females few opportunities for energy storage. Low air temperature and reduced hours of sunlight in areas with harsh climatic conditions, such as the mountains or high latitude zones, may mean fewer opportunities for finding food and reduced digestion efficiency. Under these conditions the energy needed for reproduction probably depends not only on the year the female reproduces but also on the amount of energy stored during the previous year (capital breeding strategy). This need for energy storage could be related to specialised structures such as the abdominal fat bodies. These structures have been identified in populations of this species from Central Europe (Rollinat, 1934), but do not appear in the populations studied in this paper (or in other populations of the north Iberian peninsula; Braña, 1983). Unfortunately neither the presence nor the absence of such structures is mentioned in the studies on British, Italian or Netherlands populations. The absence of abdominal fat bodies along with the evidence of annual reproduction probably means that the energy for a given event of reproduction depends mainly on the activity period of that year (income breeding strategy). It would distinguish Iberian populations (and probably other populations from southern Europe) from northern populations of this species. Although lipids contained in abdominal fat bodies represent the major lipid storage compartment (Cale and Gibbons, 1972; Scott et al., 1995; Santos and Llorente, 2001), those from other compartments may very well play a relevant role in reproduction. For instance, lipid in the carcass seems to be used when energetic resources in fat bodies are limited (Derickson, 1974), or lipids in the liver contribute to follicular growth and vitellogenesis (Bonnet and Naulleau, 1995). Scott et al. (1995) and Santos and Llorente (2001) quantified significant amounts of lipids outside abdominal fat bodies. This is why, in the population studied, stored fat used in reproduction may come from other parts of the body.

The difference in number of small females reproducing in different years might be due to differences in the weather. It is possible that the smallest adult slow worm females only reproduce in 'especially good' years. Since the 'choice' between reproducing or not reproducing is made at the beginning of the activity season (in the mating period), we consider that the energy accumulated the previous year could be an important 'argument' for this kind of females. Comparing the climate in the activity period of 2000 and 2001 we found that temperatures did not differ significantly, but there were 199 more hours of sunlight in 2001 than during the same period in 2000. On the other hand, the difference in the length of the activity period (fig. 1), with active individuals in November 1999, but not in 2000, might

also be a consequence of climate. In November, the average temperature did not substantially differ between these years, but the number of hours of sunlight did: 135 in 1999 versus 78 in 2000. Even when *A. fragilis* is considered to be a basically tigmotherm lizard (Smith, 1990), the temperature of the surfaces used depends on the sun's radiation, so we consider that the difference in sunlight hours might have an effect on the activity cycle and reproductive behaviour.

We consider *Anguis fragilis* to be a viviparous lecithotrophic species following the classification of Blackburn (2000). Females give birth to completely formed neonates and there is no evidence of the existence of an allantoplacenta (Dely, 1981). A complex corioallantoic placenta is correlated with a significant transfer of nutrients between the female and embryo, and the lack, or the presence of a simple corioallantoic placenta, indicates that there is a small amount or no transfer of nutrients (Thompson et al., 2000). Because of this and the relatively large size of ovulated ovarian follicles (personal, unpubl.), we consider that there is no major nutrient transfer to the embryo after ovulation, with most of the nutrients coming from the yolk (i.e., lecithotrophy according to Blackburn, 2000).

The incidence of dead and deformed young is very low. The behaviour of *Anguis fragilis* in captivity does not show episodes of visible excitation or stress (e.g., biting and killing the newborn) as happens with other species of similar life-histories in our latitude (e.g., *Chalcides striatus*, pers. obs.). Smith (1990) obtained considerably high values of deformed and dead young (58% of litters and 25% of total young affected). In our study we recorded 10.3% of litters affected and 2.6% of neonates. Since captivity conditions did not differ, we thought that an explanation for this discrepancy could be attributed to a poor genetic quality of individuals in the isolated population studied in southern England. New data will be necessary to compare this variable among slow worm populations.

Most of the basic variables of neonates and litters are positive and significantly correlated with female size. Litter size (number of neonates) and average neonates size increased with the female SVL. It means that bigger females give birth to more young per litter, furthermore these young are bigger, in size and mass, than the ones of smaller females. Probably these big young have higher survival rates than the small ones. Both factors: litter size and offspring size seem to favour the fitness of the bigger females offspring. In the population of southern England, Smith (1990) observed no correlation between female size and neonate size. This would indicate that the way the female distributes resources in reproduction varies among populations and suggests that the fitness of both strategies could be related to environmental temperature.

Litter mass is considered to be a good indicator of the reproductive effort in *Anguis fragilis* (Smith, 1990). Slow worm females in the populations studied in this paper made an inversion in each reproductive event (offspring mass represents, on average, 28% of female mass after the birth) similar to and slightly higher than the viviparous lizards of the same regional area: *Chalcides striatus*: 23% (P. Serantes, per. com.); *Chalcides bedriagai*: 24.5% (Galán, 2003).

Female relative litter mass in the populations studied is stable among female size. The relative clutch mass is a function of body shape and the general ecology of the lizard, with low values (0.268-0.334) in streamlined species with a flight escape-wide foraging strategy and high values (0.345-0.525) in short-robust species with cryptic behaviour and a sit and wait foraging (Vitt and Congdon, 1978). *Anguis fragilis* is a mixture of these extremes, with a streamlined body and cryptic behaviour. The relative litter mass in the population studied falls in the first category. The big size of neonates alters the body of females from its original shape. Increasing this bias may reduce its mobility, specially in the narrow spaces where these animals dwell, so the offspring size and body shape could have an effect on the low values of relative litter mass.

The productivity of young in relation to SVL (average of the number of young per mm of female SVL) is a very stable variable in the population studied. The small difference corresponding to 2000 may be due to the low number of data. It is remarkable that this variable remains practically unaltered, even though the proportion of small females that took part in reproduction ranged from 2.94% (2001) to 25% (2002). Nevertheless when the small females do reproduce, their contribution to the population, as average number of neonates, is similar (per unit of length or mass) to the larger ones.

Average litter size shows a tendency to increase from northern latitudes to the lower ones (table 4). Nevertheless, populations from the Iberian northwest studied in this paper seem to break this trend. It is interesting to note that two Spanish populations, located in a similar latitude (42°N; Asturias and A Coruña), showed very different values, even more so if we take into account that the

Table 4.

Basic reproductive variables of different slow worm populations. For each variable, the bibliographical reference (Reference), locality, latitude, altitude, year of observation, average litter size, average female reproductive frequency (F rep freq) and average annual individual female fecundity of the population (*Fi*) are shown (Braña, 1983; Patterson, 1983; Smith, 1990; Stumpel, 1985; Capula et al., 1992 and present paper).

Reference	Locality	Latitude	Altitude	Year	Litter size	F rep freq	<i>Fi</i>
Patterson, 1983	Portland island, UK	50°N	low 0-80 m	1977-1979	7.367	0.402	2.961
Smith, 1990	Purbeck island, UK	51°N	low 0-80 m	1981-1988	7.941	0.500	3.970
Stumpel, 1985	Utrecht, Netherlands	52°N	low 0-80 m	1978-1980	–	0.573	–
Capula et al., 1992	Tarvisio, Italy	45°N	high > 1000 m	1991	9.130	0.536	4.893
Braña, 1983	Asturias, Spain	43°N	medium 100-500 m	1978-1981	11.180	0.650	7.267
This paper	A Coruña, Spain	43°N	low 0-80 m	2000-2002	6.766	0.888	6.084

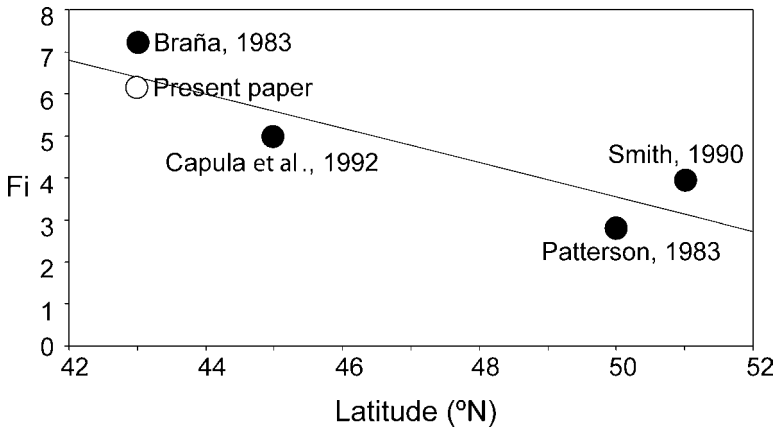


Figure 5. Average annual individual fecundity values of slow worm females (F_i) in different populations, related to the geographical latitude where there are located. Data from table 4.

population located at a higher altitude (Asturias; Braña, 1983), entailing more extreme conditions, had a litter size that was approximately 50% greater than the other, located at about sea level (A Coruña; present paper). The rate of females that take part, on average, in each reproductive event varied among populations (table 4). Combining litter size and reproductive frequency we obtained the annual average individual fecundity for females (F_i). Observing the relationship between F_i and latitude (data from Braña, 1983; Patterson, 1983; Smith, 1990; Capula et al., 1992; this paper), we found that the F_i seemed to have a tendency to increase from northern to southern populations (fig. 5). This variation could be the result of a milder climate in the localities of the latter, which permits more days of activity per year. Nevertheless, and because of the lack of data, this apparent trend must be considered carefully.

The lack of effect of the tail length on the reproductive output coincides with the results of Smith (1990) in southern England and contrasts with studies on other lizards. Dial and Fitzpatrick (1981) found that females of *Coleonix brevis* (Gekkonidae) with autotomised tails produced fewer and smaller eggs. This was also reported for other species such as *Uta stansburiana* (Fox and McCoy, 2000) or *Eulamprus quoyii* (Wilson and Booth, 1998). On the other hand, the scarce capacity of regeneration of the tail in the slow worm (Bryant and Bellairs, 1967) is not common among lizards of temperate areas, which usually have a rapid and eventually complete regeneration of the tail as *Lacerta vivipara* (Arnold, 1984). There is an association between slow tail regeneration and ecological features; Arnold (1988) shows that limbless species that burrow or live cryptically close to the earth vegetation interface or under objects tend to have a slow regeneration rate. The reduced capacity of regeneration linked to the non-effect on the reproductive output suggests that the tail does not play an important role as an energy reserve in this species. We agree with Smith's (1990) hypothesis that the main function of the tail of the slow worm is defensive as an attraction for predators and is a dispensable

part. So there is no point in regenerating it since the new one would lack the capacity of autotomy.

The sex ratio in our population is slightly biased in favour of males (approximately 1.2:1). The larger number of males may mean that some kind of competition among males must be part of the reproductive ecology. Scars on males of *Anguis fragilis* have been interpreted as a result of agonistic behaviour (Smith, 1964). On the other hand, Smith (1990) considers that these scars could be explained by other causes, such as unsuccessful attempts of predation by birds. In this study agonistic behaviour between males being transported in bags, including biting, were observed several times. Also males with bite scars were frequently captured. These marks had the size and shape of a male mouth, identical to the ones identified as mating scars in females. Therefore, we believe that agonistic encounters do occur in natural populations and may play an important role linked to reproduction. In some populations of central and northern Europe the sex ratio is significantly biased in favour of females (Stumpel, 1985; Smith, 1990; Plattenberg, 1999). In these populations females do not reproduce every year but males are assumed to reproduce every year. Bull and Shine (1979) showed that the females are the only sex affected in all known cases of reduced reproduction rates. Hence the bias of the sex ratio in these populations may compensate for the reduced number of females reproducing in a given year. If the unbalanced sex-ratio in the adult population is linked to a difference in the sex-ratio of the litters, this may be an interesting case of adaptation to cold climates. Nevertheless other populations in the same areas did not show significant bias (Smith, 1990) or even the same population in different years could change the direction of this bias (Platenberg, 1999).

Sexual maturity ages estimated for the females of the monitored population (Visma, A Coruña) is 3 years, are younger than those observed in the populations of southern England: 4 years (Smith, 1990), 5 years (Platenberg, 1999). This difference is probably due to the fact that sexual maturity is related to size more than to chronological age, as happens in studies on other lizards of the temperate region as *Lacerta vivipara* or *Podarcis bocagei* (Heulin, 1985; Bauwens and Verheyen, 1987; Galán, 1996). Maturity size is reached earlier in the Iberian populations probably because they have a greater number of activity days per year (over 300 compared to approximately 200 in the English populations; Platenberg, 1999; this paper), and a warmer climate in the active period (annual average temperature is 3.5°C higher in the A Coruña population than in the south of England, Martínez Cortizas et al., 1999; Met Office, 2003). This fact potentially allows for a greater consumption of food and higher growth rates.

We found variation among years in the size of reproductive females that gave birth in the laboratory. The average size of reproductive females ranged from 171.4 mm in 2001 to 162.4 mm in 2002. Only one pregnant female with a SVL under 140 mm was captured over the course of this study (SVL = 135 mm). These data are similar to the ones obtained by Smith (1990) and Patterson (1983). It shows that the maturity size of females may not be influenced by climatic conditions, which

indicates a proximity factor, and must be adjusted by ultimate factors such as phylogenetic constrictions while the maturity age might depend on the weather characteristics.

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