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L. Luiselli · M. Capula · R. Shine

# Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps

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## Introduction

The smooth snake, *Coronella austriaca*, is a species of the subgenus *Coronella* of the family Colubridae. It is distributed in the eastern Italian Alps, where it inhabits high-altitude environments. The species is characterized by its unique morphology and its ability to survive in harsh conditions. This study focuses on the reproductive output, costs of reproduction, and ecology of the smooth snake in this region. The research aims to understand the relationship between these factors and the snake's survival and population dynamics. The study area is located in the eastern Italian Alps, where the smooth snake is found at high altitudes. The environment is characterized by low temperatures, short growing seasons, and limited food resources. The smooth snake's reproductive strategy is adapted to these conditions, with a focus on producing a small number of large offspring. The costs of reproduction are high, and the snake's ecology is shaped by its ability to survive in these challenging environments. The study provides valuable insights into the life history and population dynamics of this species in its natural habitat.

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**Abstract** A 5-year mark-recapture study of smooth snakes (*Coronella austriaca*) in the Carnic Alps (1100 m above sea level) of north-eastern Italy provided extensive information on the biology and life-history of these small viviparous snakes. Offspring were relatively large (mean = 15 cm total length, 2.9 g) when they were born in late summer, and females grew to maturity (44 cm, 50 g) in approximately 4 years. Larger neonates retained their size advantage for at least 12 months, but did not have a higher probability of survival. Although sexual size dimorphism (at birth and at mean adult body sizes) was minor, the sexes differed significantly in several respects. Females grew faster than males during juvenile life, and adult females diverged in dietary habits from the rest of the population. Whereas juveniles (of both sexes) and adult males fed primarily on lizards, larger females shifted to feeding less frequently, but taking larger prey (mammals and snakes). Reproductive output increased strongly with maternal body size: larger females reproduced more frequently, produced larger litters of larger neonates, had higher relative clutch masses (RCMs), and had a lower proportion of stillborn offspring. Most females produced a litter every 2nd or 3rd year. We did not detect significant year-to-year variation in reproductive traits over the 5 years of our study. Females were consistent from one litter to the next in several traits (e.g., litter sizes, offspring sizes and shapes, proportions of stillborn neonates, RCMs), but this consistency was due to differences in body size among females rather than to size-independent maternal effects. Overall litter sex ratios averaged 50/50, but sex ratios tended to be more male-biased in litters that were unusually large relative to maternal body size, and in litters containing a high proportion of stillborn offspring.

L. Luiselli · M. Capula  
Department of Animal and Human Biology,  
University of Rome La "Sapienza", via A. Borelli 50,  
I-00161 Rome, Italy

R. Shine (✉)  
School of Biological Sciences A08, The University of Sydney,  
NSW 2006, Australia

"Costs" of reproduction appear to be high in this population, in terms of both energy allocation and risk. Reproduction reduced growth rates, and females that recovered condition more quickly in the year after reproduction were able to reproduce again after a briefer delay. Mortality was highest in reproducing females with high RCMs, and in females that were very emaciated after parturition. The marked increase in reproductive output with increasing maternal body size in *C. austriaca* may reflect a reduction in "costs" as females grow larger, and the dietary shift to larger prey may enhance the rate that females can accumulate energy for reproduction.

**Key words** Alpine · Colubridae · Life history · Reproduction · Reptile

## Introduction

The last two decades have seen an unprecedented expansion of field studies on the determinants of reproductive success in field populations of vertebrates. As information has accumulated, it has become obvious that many ecological and life-history traits show strong phylogenetic conservatism, so that we can only hope to understand the diversity of vertebrate life-history strategies by studying a wide phylogenetic diversity of vertebrates (e.g., Greene 1986). In practice, this means that we need more information on taxa other than birds and mammals, which have been the study organisms of choice for a high proportion of research in this field (e.g., Lott 1991). Among the reptiles, small diurnal heliothermic lizards have achieved the status of "model organisms" in behavioral ecology (Huey et al. 1983), but information on other reptilian groups has lagged far behind. Although many authors have bemoaned the logistical difficulties inherent in long-term field studies of snakes (e.g., Turner 1977), there is an emerging consensus that such studies are feasible on some taxa, and can provide invaluable information with which to test and develop life-history theory (e.g., Greene 1986; Seigel 1993). However, de-

tailed ecological information remains unavailable for most snake species, even for geographically widespread taxa that occur in parts of the world that have been subject to intensive scientific study. The smooth snake, *Coronella austriaca*, is such a species. It occurs across much of Europe, but published information on its ecology is based primarily upon studies in the extreme western limit of its range (southern England) where it is relatively rare (Spellerberg and Phelps 1977; Goddard 1984).

This paper is based on a 5-year field study of an Italian population of *C. austriaca* by two of us (L.L., M.C.). Because recapture rates of individually-marked snakes were high throughout this period, it was possible to quantify a number of factors – such as the interval between successive clutches by the same female, the consistency of offspring phenotypes in successive clutches by the same female, and the nature of “costs” faced by reproducing animals – that may affect maternal fitness, but have rarely been measured in field studies of snakes. Our aims in this paper are to describe the general ecology and reproductive biology of *C. austriaca* in the Italian Alps, to compare our results to those of previous studies on the same species in other parts of its geographic range, and to evaluate the determinants of differences among individual female *C. austriaca* in the numbers and sizes of offspring that they produced during our study. We consider not only characteristics of the females’ reproductive output, but also examine our data for evidence of “costs” of reproduction, as predicted by theoretical models for life-history evolution (e.g., Williams 1966; Shine and Schwarzkopf 1992).

## Materials and methods

### Study species

The smooth snake is a relatively slender, medium-sized (to 80 cm total length) nonvenomous colubrid species that is found over much of Europe (Arnold and Burton 1978). The species is widespread in the alpine massif and locally very common, especially in relatively dry rocky habitats. It feeds primarily upon lacertid lizards and small rodents (Andren and Nilson 1976; Goddard 1984; Rugiero et al. 1995). Unlike the congeneric oviparous *C. givondica*, the smooth snake gives birth to fully-developed live young rather than laying eggs (Agrimi and Luiselli 1994).

### Study area

We studied a population of smooth snakes at Sella Nevea, in the Tarvisio Forest among the Carnic Alps (46°26'N, 13°31'E, 1100 m elevation). The habitat consists of stonepiles and ruins of old buildings at the border of a coniferous forest. The climate is typically alpine, with prolonged snow cover each year (usually from late November to late April). Smooth snakes are abundant in this area, and are sympatric with two other snake species, adders (*Vipera berus*) and grass snakes (*Natrix natrix*). The former species has been the subject of detailed ecological studies in this area (Capula and Luiselli 1994). Male smooth snakes emerge from winter inactivity in late April (soon after the snow cover melts), with females following about 10 days later. Both sexes re-enter the hibernacula at the end of October.

## Methods

The snakes were captured by hand during daily searches along standardised routes throughout the study area. Dietary records were obtained by palpation (forced regurgitation) and by collection and analysis of faecal pellets. Females were palpated to detect the presence of oviductal offspring, and were removed from the field if they were determined to be gravid. These gravid females were maintained in small outdoor enclosures until parturition. The females were weighed daily throughout this period, and we use the mass recorded immediately prior to parturition in our analyses in the present paper. Females were maintained in their enclosures for 30 days after parturition, to record the incidence of postpartum mortality (as observed in adders: Madsen and Shine 1993; Luiselli 1992). The neonates were then released, with their mother, at her original locality of capture. All snakes were individually marked by clipping ventral scales and by paint-marking on the dorsal surface. Regeneration of clipped scales was relatively rapid, so snakes were re-clipped (and if necessary, paint-marked) each year. Our measure of body size is total length (snout-vent length plus tail).

Analyses of offspring size were based on a single mean value per litter, to avoid artificially inflating degrees of freedom in statistical tests by including litter-mates as independent replicates. However, we retained data from successive litters of individual females as separate data points for some analyses, because (i) reproductive output variables showed little consistency among successive litters within the same female (see below), and (ii) reproductive output changed considerably through a female’s reproductive life. Under these circumstances, where the level of variation among successive litters from the same female is similar in magnitude to the variance among litters from different females, data-pooling does not introduce significant artifacts into statistical analyses (Leger and Didrichson 1994). We have not used Bonferroni techniques to “correct” for spurious significance levels introduced by multiple tests, because such techniques introduce problems of subjective evaluation of “independence” of data sets, and higher type II error rates (S. Hurlbert, pers. comm.). Thus, readers should bear this caveat in mind when interpreting multiple tests on related data-sets. Relative clutch mass (RCM) was defined as maternal mass loss at parturition divided by maternal post-parturition mass (Shine 1980). We calculated the “additional mass loss at parturition” as (maternal mass loss - total neonate mass), and divided this amount by the total maternal mass loss. This variable provides a measure of the mass component of the litter that is attributable to e.g., fluids and membranes, rather than the neonates themselves. Records of prey items were obtained by palpation of freshly-captured snakes, and analysis of faeces deposited by them.

Due to the very high sampling effort, we were able to capture most adult snakes in most years. If we had often failed to capture snakes that were actually present, our data should include many examples of snakes that were recorded one year and not the next, but then “reappeared” in a subsequent year. In fact, this pattern is seen only twice in our data, out of 63 year-records for 28 snakes (Table 1).

## Results

We obtained information on 28 female *C. austriaca*, for an average of 2.25 (SD = 1.11) years each (range 1–5) and 1.07 (SD = 0.60) litters each (range 0–3).

### Ecological characteristics

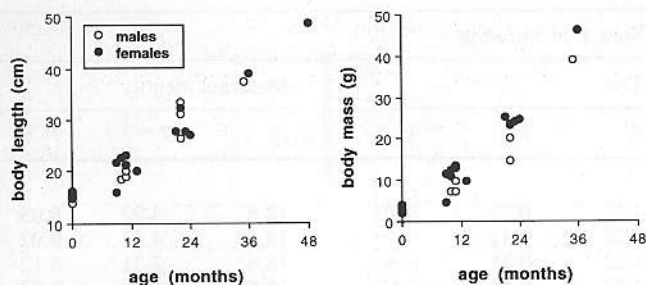
#### *Growth rates and survival of offspring*

Figure 1 shows growth data from snakes that were individually marked at birth, so that their exact age is



**Table 1** Reproductive output of smooth snakes, *Coronella austriaca*, in the Carnic Alps of Italy (*Mass pre*-maternal mass prior to parturition, *mass post*-maternal mass after parturition, % *add* *mass loss* proportional additional mass loss at parturition, beyond that attributable to neonatal mass, *date of birth* days after 1 August, *nr* not reproductive in that year, *RCM* relative clutch mass).

Female		Maternal body size			Litter size	Neonatal body size		Sex ratio (% male)	RCM	% Add mass loss	Date of birth	Propn. stillborn
ID number	Year	Length (cm)	Mass pre-(g)	Mass post-(g)		Length (cm)	Mass (g)					
1	1990	48.5	52.2	37.7	3	14.73	3.07	0.33	0.39	0.58	40	0
1	1991	48.5	42.9	—	nr	—	—	—	—	—	—	—
1	1992	48.9	47.6	—	nr	—	—	—	—	—	—	—
1	1993	48.9	56.3	38.3	4	14.03	2.83	0.50	0.47	0.59	42	0.25
2	1990	60.0	80.5	51.3	8	15.20	3.69	0.57	0.57	0	33	0
2	1991	60.0	51.0	—	nr	—	—	—	—	—	—	—
2	1992	60.1	78.7	45.6	8	15.18	3.80	0.38	0.73	0.09	38	0
3	1990	51.4	49.0	—	nr	—	—	—	—	—	—	—
3	1991	51.8	65.8	43.4	6	14.60	2.93	0.75	0.52	0.27	30	0.33
3	1992	52.1	47.5	—	nr	—	—	—	—	—	—	—
3	1993	52.2	53.9	—	nr	—	—	—	—	—	—	—
3	1994	52.2	63.1	42.3	6	14.82	2.90	0.33	0.49	0.20	27	0.17
4	1990	45.0	53.6	39.6	4	15.17	2.67	0.50	0.35	0.31	37	0.5
4	1991	45.2	41.8	—	nr	—	—	—	—	—	—	—
5	1990	44.2	40.0	—	nr	—	—	—	—	—	—	—
5	1992	45.8	42.3	—	nr	—	—	—	—	—	—	—
6	1990	48.1	57.9	44.7	4	15.55	2.88	0.75	0.30	0.15	26	0
6	1991	48.1	37.4	—	nr	—	—	—	—	—	—	—
6	1992	48.7	42.1	—	nr	—	—	—	—	—	—	—
6	1993	48.9	59.2	42.7	5	15.32	2.76	0.40	0.39	0.20	33	0
7	1991	42.2	39.8	—	nr	—	—	—	—	—	—	—
8	1991	51.1	56.2	42.7	5	14.82	2.20	0.20	0.32	0.23	47	0
8	1992	51.4	49.0	—	nr	—	—	—	—	—	—	—
8	1993	51.4	57.2	38.5	5	15.36	2.40	0.60	0.49	0.56	32	0
9	1991	46.2	38.9	—	nr	—	—	—	—	—	—	—
9	1992	47.5	56.8	41.3	5	14.88	2.46	0.40	0.38	0.26	41	0
9	1994	48.5	60.5	42.9	6	14.98	2.533	0.33	0.41	0.16	37	0
10	1992	63.0	51.8	—	nr	—	—	—	—	—	—	—
10	1993	63.0	79.7	48.8	8	16.18	3.50	0.43	0.63	0.10	27	0
10	1994	63.0	62.5	44.7	5	15.08	2.58	0.75	0.40	0.38	29	0.20
11	1992	61.1	72.0	49.4	5	15.42	3.10	0.40	0.46	0.46	33	0
11	1993	61.1	54.7	—	nr	—	—	—	—	—	—	—
11	1994	61.1	65.2	43.3	7	14.91	2.80	0.71	0.51	0.12	36	0
12	1992	54.8	48.6	—	nr	—	—	—	—	—	—	—
12	1993	56.5	53.8	—	nr	—	—	—	—	—	—	—
12	1994	56.5	53.2	—	nr	—	—	—	—	—	—	—
13	1992	57.2	62.9	45.8	6	14.92	2.78	0.50	0.37	0.03	34	0
13	1993	57.7	51.4	—	nr	—	—	—	—	—	—	—
14	1992	46.2	44.8	37.3	2	13.30	2.05	1.00	0.20	0.83	34	0.50
14	1993	46.6	42.7	—	nr	—	—	—	—	—	—	—
15	1992	47.1	39.0	—	nr	—	—	—	—	—	—	—
15	1993	47.5	48.4	—	nr	—	—	—	—	—	—	—
15	1994	47.5	51.1	35.3	4	13.80	2.20	0.00	0.45	0.80	41	0.50
16	1992	42.3	36.8	—	nr	—	—	—	—	—	—	—
16	1993	43.5	34.9	—	nr	—	—	—	—	—	—	—
16	1994	43.5	47.1	37.4	3	14.10	2.40	0.50	0.26	0.35	52	0.33
17	1992	66.4	69.2	—	nr	—	—	—	—	—	—	—
17	1993	66.4	78.6	53.1	8	15.34	2.65	0.50	0.48	0.20	40	0
17	1994	—	—	—	nr	—	—	—	—	—	—	—
18	1993	39.8	36.4	—	nr	—	—	—	—	—	—	—
19	1993	48.5	52.2	40.6	nr	14.65	2.80	0.00	0.29	—	34	—
19	1994	48.6	49.1	—	nr	—	—	—	—	—	—	—
20	1993	62.8	72.3	43.9	7	15.80	3.53	0.43	0.65	0.15	44	0
21	1993	50.2	51.8	—	nr	—	—	—	—	—	—	—
21	1994	50.3	58.4	43.8	4	15.30	2.98	0.25	0.33	0.23	38	0
22	1993	47.3	—	—	3	—	—	—	—	—	41	0.33
23	1993	52.8	45.6	—	nr	—	—	—	—	—	—	—
23	1994	53.2	57.8	41.3	4	16.45	3.75	1.00	0.40	0.10	44	0.50
24	1994	50.5	53.8	43.2	2	15.30	3.25	0.50	0.24	0.63	32	0
25	1994	53.9	—	—	6	—	—	—	—	—	—	—
26	1994	59.8	—	—	7	—	—	—	—	—	—	—
27	1994	37.5	34.0	—	nr	—	—	—	—	—	—	—
28	1994	48.7	56.2	44.9	3	15.00	2.80	1.00	0.25	0.35	40	0.33



**Fig. 1** Growth curves of individually-marked smooth snakes, *Coronella austriaca*. All of these snakes were individually marked at birth, so their ages are known exactly. See text for statistical tests

known. The variation among individual snakes in growth rates (Fig. 1) was partly due to sex. A one-factor analysis of covariance of the recapture data (with sex as the factor, age in months as the covariate, and ln body size as the dependent variable) showed that males grew more slowly than females (for ln length, slopes  $F_{1,15} = 5.21$ ,  $P < 0.04$ ; for ln mass, slopes  $F_{1,15} = 6.08$ ,  $P < 0.03$ ; see Fig. 1). Also, snakes that were larger at birth retained this size advantage at 12 months of age (linear regression of body mass at 12 months on mass at birth:  $n = 10$ ,  $r = 0.63$ ,  $P < 0.05$ ), but the increment in body mass was independent of size at birth ( $n = 10$ ,  $r = 0.47$ ,  $P = 0.18$ ). The effects of sex and size at birth on subsequent body size were independent, because males and females did not differ in size at birth (see below). The mean sizes of offspring that survived (as judged by recapture in later years) were no different from the average sizes of offspring that were never recaptured (unpaired two-tailed  $t$ -tests: for length at birth,  $t = 0.17$ ,  $df = 128$ ,  $P = 0.87$ ; for mass at birth,  $t = 0.56$ ,  $df = 138$ ,  $P = 0.57$ ).

*Age and size at maturity*

The smallest female to produce offspring in our study was 43.5 cm total length (47.1 g preparturition). The largest female was 66.1 cm and 78.6 g. Thus, based on growth rates (Fig. 1), we infer that female *C. austriaca* on our study area generally give birth for the first time in the 4th summer after they are born (i.e., at 48 months of age). This inference is supported by data on one female (28 in Table 1) that was marked at birth (September 1990) and recaptured in each subsequent year. She reproduced for the first time in 1994, at 4 years of age. Based on body sizes of mating males, the age at first reproduction is likely to be around 4 years in this sex also.

*Food habits*

118 prey items were identified from the alimentary tracts of freshly captured smooth snakes (Table 2). Contingency-table analysis revealed a significant ontogenetic shift in dietary composition: small snakes (< 30 cm long) ate

**Table 2** Prey items identified from smooth snakes, *C. austriaca*, according to sex and body length. These items were obtained by palpation of the abdomen, or from faeces produced by the snake. All items were collected in the period from July to early September, between 1987 and 1994

Prey type	Male snakes		Female snakes	
	<30 cm	>30 cm	<30 cm	>30 cm
<b>Invertebrates</b>				
Oligochaetes	0	0	1	0
Orthopterans	2	0	1	0
<b>Lizards</b>				
<i>Anguis fragilis</i>	3	11	1	8
<i>Lacerta vivipara</i>	11	46	8	16
<b>Snakes</b>				
<i>Coronella austriaca</i>	0	0	0	2
<i>Vipera berus</i>	0	0	0	1
<b>Mammals</b>				
<i>Apodemus (Sylvoemus) sylvaticus</i>	0	2	0	5

invertebrate as well as vertebrate prey, whereas larger snakes fed only on vertebrates ( $\chi^2 = 15.66$ , 4  $df$ ,  $P < 0.004$ ). However, feeding frequencies (as judged by the proportion of snakes with identifiable prey in their stomachs when collected) did not change with snake body size ( $\chi^2 = 0.71$ , 1  $df$ ,  $P = 0.40$ ). Among large snakes (> 30 cm body length), the sexes differed in terms of the prey types they consumed ( $\chi^2 = 6.84$ , 2  $df$ ,  $P < 0.03$ ) as well as their feeding frequencies:  $\chi^2 = 7.94$ , 1  $df$ ,  $P < 0.005$ ). No such sex differences were evident in smaller snakes (< 30 cm; prey types  $\chi^2 = 1.95$ , 3  $df$ ,  $P = 0.58$ ; feeding rates  $\chi^2 = 0.29$ , 1  $df$ ,  $P = 0.59$ ). The sex differences in larger snakes resulted from a tendency for males to feed often, on relatively small prey (especially lizards) whereas females fed less often, and tended to take larger prey (snakes and mammals: see Table 2). This dietary difference between the sexes also reflected a habitat difference, with females tending to occur in drier habitats than did males (L. Luiselli and M. Capula, unpublished work).

*Reproductive output*

*Annual variation*

Year-to-year variation was examined using one-factor analysis of variance, with year as the factor. This procedure revealed no significant annual variation in mean values for litter size, offspring size, offspring body shape, date of parturition, RCM, sex ratio, or the proportion of stillborn neonates (Table 3). Because maternal body size strongly influences reproductive output in this species (see below), we also computed size-corrected scores for variables that were significantly associated with maternal body size. These scores (residuals from the linear regression of the trait on maternal body length) similarly showed no significant temporal variation (Table

**Table 3** Influence of maternal identity and year on characteristics of reproductive output in smooth snakes, *C. austriaca*, in the Carnic Alps. The table gives values from single-factor analyses of variance, with either maternal identity or year as the factors. The *uncorrected variables* are raw scores, whereas the *size-corrected variables* are residual scores from the linear regression of some trait on maternal body length. Significant *P* values in bold type

Trait	Source of variation					
	Year			Maternal identity		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
<i>Uncorrected variables</i>						
Mean offspring length (cm)	4,22	0.54	0.70	18,8	3.92	<b>0.03</b>
Mean offspring mass (g)	4,22	0.42	0.79	18,8	4.42	<b>0.02</b>
Parturition date	4,22	0.25	0.90	18,8	2.31	0.12
RCM	4,22	0.70	0.60	18,8	4.30	<b>0.02</b>
% Additional mass loss	4,22	0.10	0.98	18,8	3.14	0.052
Litter sex ratio	4,22	0.29	0.88	18,8	1.42	0.31
% Live neonates	4,22	0.68	0.61	18,8	6.24	<b>0.006</b>
<i>Size-corrected variables (residual scores)</i>						
Offspring body shape (residual ln mass/length)	4,22	0.39	0.81	18,8	15.88	<b>0.002</b>
Maternal body shape (ln mass/length)						
Pre-parturition	4,22	1.03	0.41	18,8	1.05	0.50
Post-parturition	4,22	0.55	0.70	18,8	1.10	0.47
Relative fecundity (clutch size/maternal length)	4,22	0.67	0.63	18,8	1.59	0.26
Relative RCM	4,22	0.63	0.65	18,8	1.24	0.40
Relative offspring size (neonate size/maternal length)						
Based on neonate length	4,22	0.80	0.54	18,8	2.84	0.07
Based on neonate mass	4,22	0.75	0.57	18,8	3.20	<b>0.049</b>

3). We repeated the size-corrected analyses using one-factor analysis of covariance (with year as the factor, and maternal body length as the covariate) and again found no significant temporal variation in any of these traits ( $P > 0.50$  in each case).

#### Frequency of reproduction

The frequency of reproduction in snakes is often estimated by the proportion of adult-size females that are reproductive (e.g., Seigel and Ford 1987; Capula et al. 1992). In our study, we obtained a total of 63 "snake-years" of records (i.e., counting each female as a separate data point in each year she was collected). Reproductive females comprised 31 (= 49%) of these records, suggesting a biennial cycle in individual females (Table 1). However, this estimate may be biased if reproductive females modify their behaviour (e.g., bask more often) in such a way that they are easier to find and catch (Rugiero et al. 1994). Recapture records of individual females over a number of years offer a more reliable indication of the true frequency of reproduction (Brown 1991). We obtained six records of full reproductive cycles (i.e., including 2 reproductive years and the interval between). Four of these cycles (including two in one female) were biennial, two were triennial, and one female reproduced in 2 successive years. Another two females were nonreproductive in 2 successive years (so were triennial at best) and a third female was nonreproductive in 3 successive years (suggesting a quadriennial cycle, or perhaps even longer). Hence, our data suggest that biennial and triennial cycles are equally common, with oc-

casional females reproducing at longer or shorter intervals.

#### Litter size

Our female *C. austriaca* produced litters of two to eight offspring, with a mean of 5.0 (SD = 1.81,  $n = 28$ ). The primary determinant of litter size was maternal body size, with larger females producing larger litters (Fig. 2). Because adult females continued to grow between successive litters (see above), litter size also tended to increase ontogenetically within individual females (of seven females with more than one litter, the number of offspring increased in four, remained constant in two, and decreased in one). Maternal "body condition" (residual score from the linear regression of pre-parturition mass to maternal body length) also correlated positively with litter size (Table 4), because a significant proportion of the female's mass at this time consists of the litter. This correlation disappeared when litter size was compared to maternal mass post-parturition (Table 4). The proportional loss of additional material at parturition was negatively correlated with litter size ( $n = 27$ ,  $r = -0.69$ ,  $P < 0.001$ ): that is, the additional mass loss was lower (as a proportion of litter mass) for larger litters.

Are individual females consistent in relative fecundity, such that some tend to have consistently high residual scores whereas others have low scores? Apparently not. A one-factor analysis of variance (with maternal identity as the factor, and the residual fecundity score as the dependent variable) failed to detect significant differences among females in this respect (Table 3).





### Offspring shape

Analysis of residuals showed that females differed consistently in the shape of their offspring (Table 3). Analysis of covariance of offspring shape (with maternal identity as the factor, offspring length as the covariate, and offspring mass as the dependent variable) confirmed the existence of significant differences in the length to mass relationships of offspring born to different females (slopes heterogeneous:  $F_{19,89} = 2.42$ ,  $P < 0.003$ ).

### Sex ratio in litters

Overall sex ratio averaged 0.50 (SD = 0.26,  $n = 28$  litters), with individual litters varying from 0% to 100% sons. Most of the factors we measured were not correlated with offspring sex ratios (Table 4). There were no consistent differences in offspring sex ratio among females (Table 3), and no consistent ontogenetic shift in sex ratios of offspring in successive clutches produced by the same female (as has been reported in adders: Madsen and Shine 1992b): the proportion of male offspring increased from one litter to the next in three females, and decreased in four others.

Sex ratios in the litter tended to be more male-biased in litters with a higher proportion of stillborn (and hence, unsexable) neonates (Table 4). Another possible correlate of offspring sex ratio was the duration of the preceding reproductive cycle. Females that delayed for longer periods between successive litters tended to produce a lower proportion of sons, and this trend fell just below the conventional level of statistical significance ( $n = 10$ ,  $r = -0.63$ ,  $P = 0.053$ ).

### Relative clutch mass

Larger females had higher RCMs (Table 4; Fig. 2). Unsurprisingly, RCMs were higher with larger litters relative to maternal body size (using residual scores:  $n = 27$ ,  $r = 0.50$ ,  $P < 0.009$ ) and with larger offspring (Table 4). The proportional additional mass loss at parturition was negatively correlated with RCM ( $n = 27$ ,  $r = -0.41$ ,  $P < 0.035$ ): that is, larger litter masses (relative to maternal mass) were composed primarily of offspring rather than associated membranes and fluids. Females that produced an unusually high RCM at their first litter were more likely to do so again at their next reproductive bout (Table 3). Females with higher RCMs tended to be those that were in good condition prior to parturition, but were not in consistently poorer condition after parturition (Table 4).

### "Costs" of reproduction

#### Energy costs

The biomass of offspring produced by *C. austriaca* is large relative to maternal mass (mean RCM = 42%,

SD = 13%), and hence, may constitute a significant energy cost. Additionally, reproducing females allocate energy to their litter rather than to growth, so that growth rates (in maternal body length) tend to be lower in reproductive years than in nonreproductive years (true for four of five females, binomial test,  $P = 0.19$ ). This reduction of growth rate is more obvious in the year following reproduction, suggesting that females must replenish their energy reserves before beginning significant growth (in each of eight females, mass increments were lower in the year immediately following reproduction than in other nonreproductive years: binomial test,  $P < 0.005$ ). Most individual female *C. austriaca* reproduce less than annually (see above), perhaps because of such costs. If energy costs are important determinants of the duration of the nonreproductive period between reproductive years, we might expect to see that reproduction is delayed if females allocate more energy to the current litter, are more emaciated after producing that litter, or gather energy slowly after reproduction. In practice, our data suggest that the main determinants of cycle duration are a female's body size (maternal length versus cycle length:  $n = 9$ ,  $r = -0.77$ ,  $P < 0.01$ ) and her rate of increase in mass during the year following parturition (mass increment versus cycle length:  $n = 9$ ,  $r = 0.64$ ,  $P < 0.03$ ). That is, larger females reproduce more frequently, especially if they replenish their energy reserves rapidly after reproduction.

Most of the other variables that we measured showed no obvious relationship with cycle length. Measures of reproductive output (litter size, litter size relative to maternal length, offspring size, RCM) and maternal body condition after parturition were not significantly correlated with cycle length ( $P > 0.50$  in all comparisons). Similarly, the duration of the cycle preceding reproduction was not significantly correlated with any of these measures either ( $P > 0.50$ ). Thus, it appears that variation among females in reproductive traits has little effect on, nor is it affected by, the duration of the nonreproductive period between successive litters. Instead, it seems that females simply delay reproduction until they have accumulated sufficient energy reserves (maternal condition preparturition is independent of the duration of the preceding nonreproductive phase:  $n = 8$ ,  $r = 0.58$ ,  $P = 0.13$ ).

#### Survival costs

Given our high recapture rates of marked snakes among years, it is probable that females who disappeared from the population had died. We observed mortality of adult female snakes on eight occasions: four of our snakes died in captivity 4–8 days after parturition, and four were killed by humans (including three found dead on the road). Contingency-table analysis revealed significant annual variation in mortality rates among the four years of the study ( $\chi^2 = 8.35$ , 3 *df*,  $P < 0.04$ ). Overall, gravid females survived as well as nongravid females ( $\chi^2 = 0.03$ , 1 *df*,  $P = 0.87$ ), but more detailed analysis shows



that death after parturition was more likely to occur in females that were emaciated after giving birth (comparing residual scores of postparturition mass to maternal length between survivors and nonsurvivors: unpaired one-tailed  $t = 2.50$ , 16 *df*,  $P < 0.019$ ) and in females that produced high RCMs (unpaired one-tailed  $t = 2.09$ , 16 *df*,  $P < 0.027$ ).

## Discussion

Although our study is based on a relatively small number of animals (Table 1), the long timescale of the study and the high recapture frequency for individuals have enabled us to obtain a clear picture of many ecological and reproductive phenomena within the population. Broadly speaking, our alpine population of *C. austriaca* resembles previously studied populations from other parts of the species' range in terms of fundamental ecological and life-history traits such as dietary composition, adult body sizes, litter sizes, neonate sizes, age at maturation, and seasonality of reproduction (Duguy 1961; Andren and Nilson 1976; Spellerberg and Phelps 1977; Goddard and Spellerberg 1980, Goddard 1984). For example, the mean litter size in our study (5.0) was intermediate between mean values reported for populations in southern Britain (3.9: Goddard and Spellerberg 1980) and western France (8.3: Duguy 1961). However, our data enable us to look at underlying processes in more detail than has been possible in previous work on this taxon. The lack of significant annual variation in reproductive traits over the 5 years of our study (Table 3) – possibly due to the wide dietary breadth of this population (Table 2), and the consequent ability to switch between alternative prey types as they vary in abundance – removes a factor that has complicated previous analyses.

One main theme to emerge from our work is the complex interplay of trophic ecology and reproductive biology, and the resultant allometry in reproductive output of female *C. austriaca* (Fig. 2). It is commonly (perhaps universally) true that reproductive output increases with maternal body size in snakes, but this increase is generally due to increases in only two traits: litter size and reproductive frequency (e.g., Blem 1982; Seigel and Ford 1987). Reptilian RCM usually remains relatively constant over a wide range of maternal body sizes in intraspecific comparisons (Pianka and Parker 1975; Seigel et al. 1986), whereas *C. austriaca* showed a very strong (seven-fold; Fig. 2) increase in RCM with maternal body length. Although many life-history models predict that reproductive effort (RE) should increase with maternal age and size (see Roff 1992 for a review), RCM probably offers only a weak index of RE for most reptiles (Vitt and Congdon 1978; Shine and Schwarzkopf 1992). The general constancy of squamate RCM over a wide range of maternal body sizes has been interpreted as evidence for physical constraints on abdominal volume available to hold the clutch (e.g., Vitt and Congdon 1978), but this factor clearly cannot explain the size-related shift in RCMs of *Coronella* (Fig. 2).

Why is reproductive output so much higher in large female *C. austriaca* than in smaller conspecifics? Life-history theory suggests that optimal levels of reproductive investment depend on the balance between fitness "benefits" (numbers and viability of offspring produced) and "costs" (decrements to a female's ability to survive and reproduce again, and her reproductive output at those subsequent episodes) (e.g., Williams 1966; Roff 1992). It is difficult to see why maternal body size should influence the "benefit" derived from equivalently sized offspring, so that an investigation of possible allometry in "costs" seems worthwhile. Our data suggest that "costs" of reproduction are high in this population, in terms of both energy and survival. The existence of significant energy costs is evident from the dependence of reproductive frequency on the rate of maternal growth (and hence, ability to accumulate energy). The existence of survival costs is evident from the higher mortality rates of females that produce large RCMs, and females that are in poor condition after parturition. Additionally, the difference in our estimates of female reproductive frequency based on direct sampling of females in the population, versus derived from mark-recapture records over longer time periods, suggests that females are more easily captured during years in which they are reproductive. Gravid female smooth snakes generally bask in positions where they are fully exposed to the sun's rays, whereas males and nonreproductive females elevate their body temperatures by sheltering beneath flat rocks that are warmed by the sun (L. Luiselli and M. Capula, unpublished work). Enhanced visibility of gravid females, due to prolonged basking by such animals, has been documented in several other viviparous reptile species living in cold climates (Peterson et al. 1993), including the sympatric lizard *Anguis fragilis* (Capula and Luiselli 1993). Females that are more easily caught by us may also have been more visible to other predators, although we cannot be sure that this is the case (Andren 1985; Madsen and Shine 1993). Additional support for the hypothesis of greater vulnerability of gravid females to predation comes from our observations on another population of *C. austriaca*: reproducing females constituted 13 of 15 smooth snakes that we found dead (killed by predators) over the period 1985–1994 in central Italy (Tolfe Mountains, Province of Rome).

Given that costs of reproduction are high for female *C. austriaca*, the most plausible advantages from increasing reproductive output with increasing body size involve a reduction in such costs for larger animals. If a high proportion of mortality "costs" comes from predation, larger body size may directly reduce a female's vulnerability to predation by making her a more formidable potential prey item. Hence, a larger female could "afford" to have a higher RCM, and be more emaciated after parturition, without incurring as high a risk of mortality as an equivalent smaller female. We note, however, that this assumption may not be realistic (e.g., if birds such as *Buteo buteo* are important predators at Sella Nevea, as seems to be the case, they may not be deterred

from attacking even the largest smooth snake). Secondly, energy costs may be lower for larger animals. Adult female *C. austriaca* in our population showed a significant dietary shift away from lizards (the most common prey for juveniles of both sexes, and for adult males) to much larger prey: snakes and mammals. Adult females also showed a decrease in feeding frequency, suggesting a shift towards reliance on infrequent large prey rather than more abundant smaller prey items (Table 2). We suggest that female *C. austriaca* may utilise ambush predation, a strategy that may be unsuited to adult males because of their need to engage in prolonged mate-searching movements during the mating season (Strijbosch and Van Gelder 1993). Similar dietary divergence between the sexes has been reported in several other snake species, but generally in association with significant sexual dimorphism in adult body sizes (e.g., Zinner 1985; Shine 1986). In the case of *C. austriaca*, males and females attain similar adult body sizes (Waitzmann and Sandmaier 1990), so that the dietary divergence between the sexes cannot be interpreted as a secondary consequence of body-size dimorphism. Whatever its cause, the ontogenetic dietary shift in females to larger prey may significantly enhance energy intake, and thus allow larger females to reproduce more frequently, with larger litters of larger offspring (Fig. 2). Also, the physical burden of a high RCM may be less "costly" to an ambush forager (because mobility is relatively unimportant) than to a predator that relies on searching actively for its prey. Thus, larger females may enhance their reproductive output for two reasons: higher feeding rates and lower associated costs.

The ontogenetic shift in reproductive output in *C. austriaca* also involves a considerable increase in offspring size with maternal body size (Fig. 2). Similar intraspecific correlations between maternal body size and offspring size occur in many types of animals (Roff 1992), including some reptiles (e.g., Stewart 1979), but are generally much less marked than in *Coronella*. Given the anatomy of the pelvic area in snakes, physical constraints related to pelvic aperture (e.g., Congdon and Gibbons 1987) cannot explain such a correlation in *Coronella*. Life-history models predict such correlations under assumptions involving density-dependent mortality (Parker and Begon 1986) or selection on clutch sizes (McGinley 1989), but detailed data are needed to evaluate the applicability of such assumptions to the study organism in question (Roff 1992). In the case of *C. austriaca*, our data suggest that larger size at birth does not influence survival of juveniles, but does enhance body size at later ages. Given the considerable reproductive advantages of larger body size, at least in females (Fig. 2), larger neonates may thereby benefit in terms of lifetime reproductive success. A more detailed evaluation of the causes and consequences of ontogenetic shifts in offspring size must await further data on this population.

Returning to the concept of "costs" of reproduction in our population, our data suggest not only that female smooth snakes experience both energy and survival

costs, but also that the two are closely related. Some component of the survival costs of reproduction may be independent of energy expenditure (e.g., the apparently higher catchability of reproductive versus nonreproductive females), but at least two energy-related measures (RCM, and degree of maternal emaciation after parturition) are significant predictors of maternal survival. These two energy measures are not significantly correlated with each other, suggesting that survival costs may accrue during gestation (with a higher RCM reducing maternal mobility, and thus, ability to evade predators; Seigel et al. 1987) as well as after parturition (perhaps because of starvation, or because emaciated females are vulnerable to predators when they begin moving around to forage; Madsen and Shine 1993). Similarly high mortality rates immediately after parturition have been reported in female adders (Capula et al. 1992; Madsen and Shine 1993). The occurrence of significant reproductive costs is consistent with theoretical models for the evolution of low frequencies of reproduction (Bull and Shine 1979), as observed in this population and in sympatric adders (Capula and Luiselli 1994). Interactions between energy costs and survival costs are also of considerable interest from a theoretical perspective, because they bear directly on current debates on the measurement of reproductive effort (RE). Energy-based measures of RE are most likely to be useful if there is a strong relationship between the magnitude of costs paid in these two different currencies (Shine and Schwarzkopf 1992), as seems to be true in *C. austriaca*. The lack of a significant trade-off between litter size and offspring size in *C. austriaca* is consistent with the observed allometry of RCMs in this species. The existence of such a tradeoff would have suggested that space to hold the developing embryos imposes a finite limit on litter volume, but such a constraint would be incompatible with the observed wide range of RCMs in reproducing females of this taxon (Fig. 2).

Extensive data on a small population of adders (*Vipera berus*) in the extreme southern tip of Sweden suggested that the most important determinant of lifetime reproductive success in females was likely to be the rate at which they could accumulate energy (Madsen and Shine 1992a). The same may well be true of our *C. austriaca* population. The considerable reproductive (= fitness) advantages of large female size may be responsible for the observed growth trajectories, with females growing faster than males even during juvenile life (Fig. 1). Growth rates are also higher in juvenile females than in juvenile males in the adders (for Sweden, Madsen and Shine 1992a; Madsen et al. 1993; for Sella Nevea, L. Luiselli and M. Capula, unpublished work). However, our smooth snakes differed from the Swedish adders in important respects. For example, our analyses provided little evidence of strong maternal effects, apart from those exerted by maternal body size. If body-size effects were removed, successive litters from individual females showed little consistency in terms of relative litter sizes, offspring sizes, RCMs, or litter sex ratios (Table 3). One trait that did vary consistently was offspring body shape



(mass/length) but experimental work suggests that variation in this trait might reflect thermal conditions during embryogenesis (basking frequency) rather than genetic factors (Shine and Harlow 1993). Thus, females may differ consistently in offspring shape simply because some females live in areas with greater basking opportunities.

Although our data reveal a number of patterns in reproductive output of *C. austriaca*, much remains to be learned. Several of our results are intriguing, but inexplicable at present. For example, correlations between litter sex ratio and other variables (such as relative litter size, reproductive frequency and the incidence of stillborn neonates) suggest that female smooth snakes may somehow manipulate litter sex ratios – perhaps through selective mortality of daughters *in utero* (note that the surviving offspring from litters with many stillborn young are mostly sons). However, the adaptive significance of such sex-ratio manipulation (if, indeed, there is any such significance) remains obscure. Similarly, we are puzzled by the increase in offspring size with increasing maternal size (especially since our data did not reveal any enhanced survival of larger neonates) and the surprising constancy in dates of parturition across years with different weather conditions (and thus, we would suspect, different basking opportunities). The changes from year to year in the survival rates of adult females are unexplained. Differences in growth rates of juvenile males and females, prior to any sex differences in resource allocation to reproduction, remain difficult to understand in terms of optimality models. And finally, we note that further information on the proximate causes of mortality in this population would be of great value. The data gathered so far suggest that *C. austriaca* may offer a useful model system in which to investigate the complex interaction between resource accrual, reproductive output, and the consequences of various levels of reproductive expenditure on an organism's survival and subsequent reproductive success.

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## References

- Agrimi U, Luiselli L (1994) Ecology of the snake *Coronella girondica* (Reptilia:Colubridae) in central Italy. *Vie Milieu* 44:203–210
- Andren C (1985) Risk of predation in male and female adders, *Vipera berus* (Linné). *Amphib-Reptil* 6:203–206
- Andren C, Nilson G (1976) Hasselsnoken (*Coronella austriaca*) – en utrottningsshotad ormart! *Fauna Flora* 2:61–76
- Arnold EN, Burton JA (1978) A field guide to the reptiles and amphibians of Britain and Europe. Collins, London
- Blem CR (1982) Biennial reproduction in snakes: an alternative hypothesis. *Copeia* 1982:961–963
- Brown WS (1991) Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. *Herpetologica* 47:101–115
- Bull JJ, Shine R (1979) Iteroparous animals that skip opportunities for reproduction. *Am Nat* 114:296–316
- Capula M, Luiselli L (1993) Ecology of an alpine population of the slow worm, *Anguis fragilis* Linnaeus 1758. Thermal biology of reproduction. *Herpetozoa* 6:57–63
- Capula M, Luiselli L (1994) Reproductive strategies in alpine adders, *Vipera berus*. The black females bear more often. *Acta Oecol* 14:207–214
- Capula M, Luiselli L, Anibaldi C (1992) Complementary study on the reproductive biology in female adder, *Vipera berus* (L.), from eastern Italian Alps. *Vie Milieu* 42:327–336
- Congdon JD, Gibbons JW (1987) Morphological constraint on egg size: a challenge to optimal egg size theory? *Proc Natl Acad Sci USA* 84:4145–4147
- Duguy R (1961) Le cycle annuelle d'activité de *Coronella austriaca* Laur.; d'après les observations manuscrites inédites de Raymond Rollinat. *Terre Vie* 15:401–435
- Goddard P (1984) Morphology, growth, food habits and population characteristics of the smooth snake *Coronella austriaca* in southern Britain. *J Zool Lond* 204:241–257
- Goddard P, Spellerberg IF (1980) Reproduction as a factor in the conservation of *Coronella austriaca* in southern England. *Bull Ecol* 11:535–541
- Greene HW (1986) Natural history and evolutionary biology. In: Feder ME, Lauder GV (eds) *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates*. University of Chicago Press, Chicago, pp 99–108
- Huey RB, Pianka ER, Schoener TW (1983) Lizard ecology: studies of a model organism. Harvard University Press, Cambridge
- Leger DW, Didrichson IA (1994) An assessment of data pooling and some alternatives. *Anim Behav* 48:823–832
- Lott DF (1991) Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge
- Luiselli L (1992) Reproductive success in melanistic adders: a new hypothesis and some considerations on Andren and Nilson's (1981) suggestions. *Oikos* 64:601–604
- Madsen T, Shine R (1992a) Determinants of reproductive success in female adders, *Vipera berus*. *Oecologia* 92:40–47
- Madsen T, Shine R (1992b) Sexual competition among brothers may influence offspring sex ratio in snakes. *Evolution* 46:1549–1552
- Madsen T, Shine R (1993) Costs of reproduction in a population of European adders. *Oecologia* 94:488–495
- Madsen T, Shine R, Loman J, Håkansson T (1993) Determinants of mating success in male adders, *Vipera berus*. *Anim Behav* 45:491–499
- McGinley MA (1989) The influence of a positive correlation between clutch size and offspring fitness on the optimal offspring size. *Evol Ecol* 3:150–156
- Parker GA, Begon M (1986) Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am Nat* 128:573–592
- Peterson CR, Gibson AR, Dorcas ME (1993) Snake thermal ecology: the causes and consequences of body-temperature variation. In: Seigel RA, Collins JT (eds) *Snakes: ecology and behavior*. McGraw-Hill, New York, pp 241–314
- Pianka ER, Parker WS (1975) Age-specific reproductive tactics. *Am Nat* 109:453–464
- Roff DA (1992) The evolution of life histories. Chapman and Hall, New York
- Rugiero L, Capula M, Luiselli L (1994) Scelta dell'habitat in una popolazione alpina di *Coronella austriaca* (Reptilia, Colubridae) in relazione allo stato riproduttivo. *Boll Mus Reg Sci Nat Torino* 12, in press
- Rugiero L, Capula M, Filippi E, Luiselli L (1995) Food habits of Mediterranean populations of the smooth snake, *Coronella austriaca*. *Herpetol J*, (in press)
- Seigel RA (1993) Summary: future research on snakes, or how to combat "lizard envy". In: Seigel RA, Collins JT (eds) *Snakes: ecology and behavior*. McGraw-Hill, New York, pp 395–402
- Seigel RA, Ford NB (1987) Reproductive ecology. In: Seigel RA, Collins JT, Novak SS (eds) *Snakes: ecology and evolutionary biology*. Macmillan, New York, pp 210–252



- Seigel RA, Fitch HS, Ford NB (1986) Variation in relative clutch mass in snakes among and within species. *Herpetologica* 42:179–185
- Seigel RA, Huggins MM, Ford NB (1987) Reduction in locomotor ability as a cost of reproduction in snakes. *Oecologia* 73:481–465
- Shine R (1980) "Costs" of reproduction in reptiles. *Oecologia* 46:92–100
- Shine R (1986) Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* 69:260–267
- Shine R, Harlow P (1993) Maternal thermoregulation influences offspring viability in a viviparous lizard. *Oecologia* 96:122–127
- Shine R, Schwarzkopf L (1992) The evolution of reproductive effort in lizards and snakes. *Evolution* 46:62–75
- Spellerberg IF, Phelps TE (1977) Biology, general ecology and behaviour of the snake, *Coronella austriaca* Laurenti. *Biol J Linn Soc* 9:133–164
- Stewart JR (1979) The balance between number and size of young in the live bearing lizard *Gerrhonotus coeruleus*. *Herpetologica* 35:342–350
- Strijbosch H, Van Gelder JJ (1993) Okologie und biologie der schlingnatter, *Coronella austriaca* Laurenti 1768 in den Niederlanden. *Mertensiella* 3:39–58
- Turner FB (1977) The dynamics of populations of squamates, crocodylians and rhynchocephalians. In: Gans C, Tinkle DW (eds) *Biology of the Reptilia*. Academic Press, New York, pp 157–264
- Vitt LJ, Congdon JD (1978) Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am Nat* 112:595–608
- Watzmann M, Sandmaier P (1990) Zur Verbreitung und Habitatwahl der Reptilien im Donautal zwischen Passau und Linz (Niederbayern, Oberösterreich). *Herpetozoa* 3:25–53
- Williams GC (1966) *Adaptation and natural selection*. Princeton University Press, Princeton
- Zinner H (1985) On behavioral and sexual dimorphism of *Telescopus dhara* Forscal 1776 (Reptilia: Serpentes, Colubridae). *J Herpetol Assoc Afr* 31:5–6