Food habits, growth rates, and reproductive biology of grass snakes, *Natrix natrix* (Colubridae) in the Italian Alps

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(With 2 figures in the text)

A five-year mark-recapture study at Sella Nevea, a montane (1100 m a.s.l.) site in the Carnic Alps, provided information on diets, growth rates, and reproductive output in an Italian population of the wide-ranging grass snake, *Natrix natrix*. Our snakes resembled a previously-studied population in lowland Sweden in terms of body size at sexual maturation in females (70 cm) and mean adult female body length (82 cm). However, growth rates were lower in our population, and sexual maturation was delayed (6–8 years, versus 4–5 years in Sweden), perhaps because of the cool climate and relatively brief growing period each year. Females produced a single clutch of 4–24 eggs in late July each year. Larger females produced larger clutches, but clutch size relative to maternal size was lower than in Swedish grass snakes. Hatchling sizes and Relative Clutch Masses (RCMs) did not shift with increasing female size. RCMs may provide a useful index of 'costs of reproduction' in this population, because females with high RCMs were very emaciated after oviposition, and hence may experience a greater risk of mortality, as well as a high energy expenditure. Prolonged incubation gave rise to longer, thinner hatchlings, but the low environmental temperatures at the study site may favour early hatching (and hence, result in a shorter fatter hatchling emerging from the egg, with more of its energy stores unused). Compared to sympatric viviparous snakes (*Coronella austriaca* and *Vipera berus*), the oviparous grass snakes can achieve a much higher reproductive output owing to a larger clutch size and more frequent reproduction (annual, rather than biennial or triennial). The abundant prey resource used by grass snakes (amphibians) may also enable them to recoup energy more rapidly after reproduction; dietary composition shifts ontogenetically in both sexes, with the largest prey (mice and adult toads) taken primarily by large female snakes.

Introduction

Geographic variation in life-history traits within wide-ranging species provides an exceptional opportunity to examine functional correlates of life-history diversity (e.g. Gregory, 1977). By restricting attention to variation among populations within a single species, comparisons are not confounded by major genetically-coded divergence in other morphological, behavioural, and ecological traits. With the growing awareness that many cases of divergence in life-history traits reflect phenotypic plasticity (responses to local environmental conditions) rather than population-specific genetic adaptations (e.g. Ballinger, 1977), there has been an appreciation of the value of information derived from studies of a single species over a broad range of ecological conditions. The snake taxa that have attracted most attention in this respect are colubrid species of the subfamily

Natricinae, presumably because of their abundance and wide distribution. Garter snakes (*Thamnophis* spp.) of North America have been the focus of the most detailed work (e.g. Gregory, 1977; Kephart, 1982), but at least one European natricine species (the grass snake, *Natrix natrix*) also offers ideal material for such studies: it is abundant, easily maintained in captivity, and occurs over a large area. Although some ecological data are available for Italian populations of *N. natrix* (e.g. Luiselli & Rugiero, 1991; Capula, Rugiero & Luiselli, 1994), the most extensive published ecological data on grass snakes are based primarily on populations in Sweden (Madsen, 1983, 1984, 1987a, b, Madsen & Shine, 1993b, c), which are morphologically distinct from Italian populations (Thorpe, 1973).

Materials and methods

Two of us (LL, MC) studied a population of grass snakes at Sella Nevea, in the Tarvisio Forest among the Carnic Alps (46°26'N, 13°31'E, 1100 m a.s.l), from 1987 to 1994, with most emphasis from 1990 to 1994. The study area is a mosaic of grassy pastures interspersed with stony ground at the edge of coniferous forest. The climate is typically alpine: cold winters with prolonged snow covering, and cool, rainy summers. Grass snakes are abundant in this area, and occur sympatrically with adders (*Vipera berus*) and smooth snakes (*Coronella austriaca*). Both of these species have been the subjects of detailed ecological studies in this area (Capula, Liuselli & Anibaldi, 1992; Luiselli 1992; Capula & Luiselli, 1994; Luiselli, Capula & Shine, 1996). The grass snakes enter their hibernacula (often shared with the 2 other species) in late October and emerge in mid-April, with males emerging before females. Mating commences in May, with most mating aggregations consisting of a single female accompanied by several males (Madsen & Shine, 1993b; Luiselli & Capula, unpubl. data). Females oviposit late in July. Of 17 natural nests discovered over the period 1987 to 1995, 5 were under large rocks, 3 were under wet moss, 5 were within rotting logs, and 4 were within manure piles.

Methods

The snakes were captured by hand during standardized searches along specified routes through the study area. Snakes were palpated after capture. Food items in the stomach were removed by forced regurgitation, and gravid females (identified by abdominal swelling) were removed and placed in terraria until they had oviposited. Eggs were not weighed individually, because in most cases the egg mass was strongly adherent and eggs could not be separated without damaging them. After the eggs were laid, we placed each clutch in an individual plastic container, with damp vermiculite as the substratum. The containers were placed at ground level, in full shade (to avoid desiccation of the eggs), and hence experienced a strong diurnal cycle in ambient temperatures (from approximately 16 to 27 °C each day) throughout incubation. This incubation regime resulted in hatching times very similar to those from natural nests, based on the time of first appearance of naturally-incubated hatchlings in the study area each year. The adults and offspring were released in the study area (at the female's point of original capture) within 30 days after the eggs hatched. Female mass was measured shortly prior to laying, when we noticed that females would move restlessly in search of a suitable site for oviposition. Snakes were individually marked by clipping ventral scales and by recording individual colour patterns (Madsen, 1983). Regeneration of clipped scales was relatively rapid, so snakes were reclipped each year. Our measure of body size is total length (snout-vent length plus tail).

Our statistical analyses of offspring size were based on a single mean value per clutch, to avoid artificially inflating degrees of freedom in statistical tests by including clutch-mates as independent replicates. However, we retained data from successive clutches of individual females as separate data points for some analyses, because reproductive output changed considerably through a female's reproductive life, and reproductive output variables showed little consistency among successive clutches within the same female ($P > 0.05$ for all traits in one-factor ANOVAs with maternal identity number as the factor). Because the level of variation

among successive clutches from the same female was similar in magnitude to the variance among clutches from different females, this data-pooling will not introduce significant artefacts into statistical analyses (Leger & Didrichson, 1994). Relative Clutch Mass (RCM) was defined as maternal mass loss at oviposition divided by maternal post-oviposition mass.

Results

Data were obtained from 20 females, 16 of which produced eggs over the five years of the study (Table I). Three of these females produced clutches in successive years, so we have data on a total of 19 clutches.

Body sizes and growth rates

Reproducing females ranged from 70.2 to 120.2 cm (mean = 82.1 cm, S.D. = 13.7). Recaptures of individually-marked hatchlings showed that growth was rapid for the first three years, by which time the snakes had attained body lengths of approximately 50 cm (mean = 48.9 cm, S.D. = 2.46, range = 44.9–53.3 cm, $n - 8$; see Fig. 1). There was no significant difference in mean growth rates of males and females over the first three years of life (heterogeneity of slopes test of body length vs. age, $F_{1,39} = 3.68$, $P = 0.062$; ANCOVA test for intercepts $F_{1,40} = 2.47$, $P = 0.12$). We infer that female *N. natrix* in our population reach maturity (70 cm) when they are about 6–8 years old. This estimate is based on fitting our mark-recapture data to two growth models, the von Bertalanffy curve and the logistic-by-length curve. In both cases, the model used was as follows:

recapture SVL = A − (A − initial SVL) * exp(−R * number of days between recaptures),

where A = asymptotic length and R = intrinsic growth rate (both in cm). In both cases, we used all available data (i.e. from snakes individually marked at hatching, as well as specimens first collected as subadults or adults in the field). Our data fitted the von Bertalanffy curve well ($r^2 = 0.987$), and yielded estimates of A = 77.6024 and R = 0.0006737. Fitting the same mark-recapture data to a logistic-by-length curve gave a slightly worse fit ($r^2 = 0.972$), a similar asymptotic length (A = 76.66438) and a faster growth rate (R = 0.0016). The resulting von Bertalanffy growth curve predicted that female adult size would be reached at eight years of age, whereas the logistic-by-length model predicted female maturation at six years of age.

Given the very low growth rates of adult females (Fig. 1), and the wide range in body sizes of adult females (one exceptional female measured 120 cm), some of the larger females may be very old. This inference is supported by skeletochronological ageing of one large (113.5 cm) female grass snake, found dead in an area 10 km west of Sella Nevea: based on growth rings, we estimated that she was 13 years old. However, it is also possible that some of these very large females are quite young, and very fast-growing.

Clutch sizes

The grass snakes laid an average of 9.16 eggs (S.D. − 5.43, based on 19 clutches; range = 4–24). Clutch sizes increased strongly with increasing maternal body size (Fig. 2: $n = 19$, r = 0.93, $P < 0.0001$: linear regression equation − clutch size = 0.37 [maternal length] − 21). The proportion of eggs that did not produce viable hatchlings ranged from 0–67% (mean = 34%,

TABLE I

Reproductive data on grass snakes, **Natrix natrix**, from the Italian Alps. For 'reproductive status', 0 = non-reproductive when captured, 1 = gravid

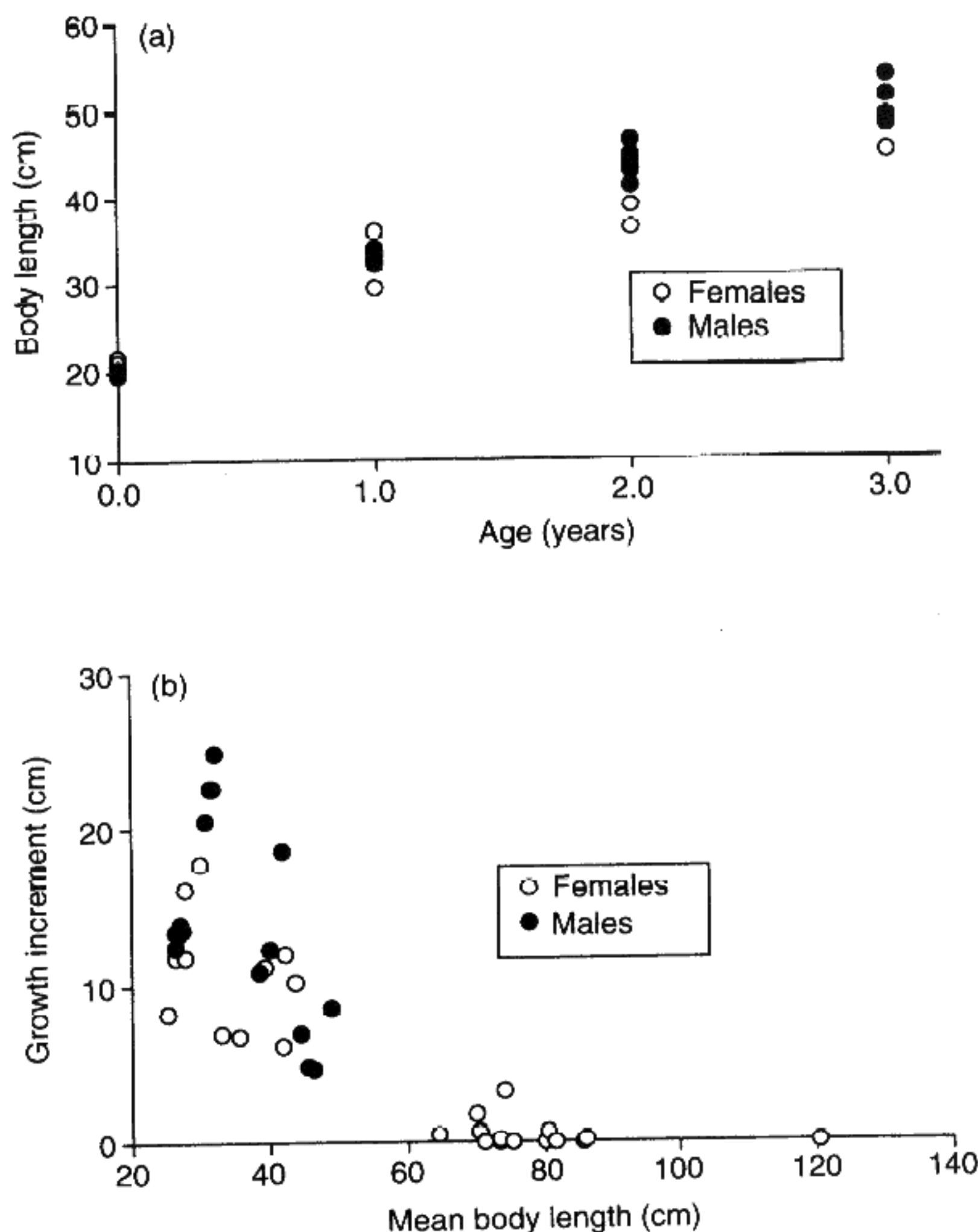| Female #	Year	Maternal length (cm)	Reproductive status	Maternal mass pre-oviposition (g)	Maternal mass post-oviposition (g)	Relative clutch mass	Clutch size (total # of eggs)	Clutch size (# of inviable eggs)	Mean mass of hatchings (g)	S.D. of hatchling mass (g)	Mean length of hatchlings (cm)	S.D. of hatchling length (cm)	Sex ratio of hatchings (% male)	Date of oviposition	Date of hatching	Incubation period (days)
1	90	85.7	0	119.3												
1	91	85.9	1	211.0	116	0.82	12	4	3.56	0.21	20.33	1.54	0.38	24 Jul.		
1	92	85.9	0	123.6												
2	90	87.2	1	224.2	122.4	0.83	9	6	3.50	0.17	20.67	0.451	1.00	19 Jul.	24 Aug.	36
3	90	69.6	0	77.4	subadult?											
3	91	72.8	0	86.9	subadult?											
3	93	82.1	1	214.1	118.3	0.81	9	5	3.20	0.40	20.08	0.26	0.25	29 Jul.	4 Sep.	37
4	90	79.5	0	106.0												
4	91	80.1	1	204.0	124.7	0.64	10	2	3.24	0.12	20.25	0.33	0.63	28 Jul.	30 Aug.	33
4	92	80.1	1	98.0	subadult?		6	4	3.85	0.07	20.90	0.14	0.50	26 Jul.	26 Aug.	31
5	90	73.5	0													
5	92	77.2	1	187.0	123.2	0.52	7	4	2.97	0.15	20.33	0.47	0.67	28 Jul.	19 Aug.	22
6	90	81.8	1	189.6	114.2	0.66	8	0	2.94	0.07	19.95	0.28	0.38	24 Jul.	22 Aug.	29
6	91	81.8	0	136.2												
7	90	67.8	0	64.2	subadult?											
7	91	69.5	0	70.9	subadult?											
7	92	70.2	1	143.9	106.2	0.36	4	2	3.15	0.07	20.25	0.21	0.50	23 Jul.	27 Aug.	35
8	90	71.3	1	170.1	92.9	0.83	10	5	2.58	0.28	19.22	0.49	0.60	20 Jul.	27 Aug.	38
8	91	71.3	0	102.0												
9	91	71.6	1	189.6	104.2	0.82	6	1	3.06	0.06	20.08	0.16	0.60	26 Jul.	2 Sep.	38
10	91	73.5	1	193.1	118.4	0.63	7	2	3.15	0.40	20.24	0.41	0.63	17 Jul.	21 Aug.	35
10	92	73.6	0	185												
10	93	73.6	1	168.0	107.3	0.57	8	0	3.75	0.55	20.88	0.40	0.25	23 Jul.	26 Aug.	34
10	94	73.6	1				6	2						19 Jul.	23 Aug.	35
11	91	120.2	0	572.3												
11	92	120.2	0	568.7												
11	93	120.2	1	765.4	507.3	0.50	23	2	3.24	0.56	20.15	0.77	0.48	22 Jul.	20 Aug.	29
12	91	68.8	0	77.2												
13	92	116.3	1	754.1	513.1	0.45	24	1	3.80	0.68	20.78	0.87	0.57	30 Jul.	6 Sep.	38
14	93	75.5	1	193.6	109.8	0.76	7	4	3.67	0.55	20.53	0.70	0.67	28 Jul.	11 Sep.	45
14	94	75.5	1	186.0	107.4	0.73	5	2	5.00	0.30	21.83	0.55	0.67	17 Jul.	26 Aug.	40
15	93	63.8	0	76.9	subadult?											
15	94	64.3	0	92.9	subadult?											
16	93	75.7	0	125.8	subadult?											
17	94	81.2	1	202.5	123.7	0.64	8	4	3.08	0.17	20.13	0.25	0.50	30 Jul.	9 Sep.	41
18	94	96.8	0	219.7												
19	94	94.1	0	219.0												
20	94	83.6	1	83.6			5	0	3.20		20.02	0.41	0.40	24 Jul.	30 Aug.	37

FIG. 1. Growth rates of individually marked grass snakes, *Natrix natrix*, at Sella Nevea in the Carnic Alps: (a) snakes of known ages (marked at hatching = age zero); (b) annual increment in total body length against mean body length during the recapture interval.

S.D. = 24%, based on 19 clutches). The proportion of non-viable eggs was not correlated with maternal body length ($n = 19$, $r = -0.35$, $P = 0.14$), mean hatchling mass ($n = 18$, $r = 0.13$, $P = 0.61$), or clutch size ($n = 19$, $r = -0.37$, $P = 0.12$).

Hatchling sizes

Hatchlings averaged 20.37 cm (S.D. = 0.54, range of 18 clutch means = 19.22–21.83) and 3.38 g (S.D. = 0.53, range of 18 clutch means = 2.58–5.00 g). Hatchling size was not significantly correlated with maternal body size ($n = 18$, $r = 0.10$, $P = 0.68$ for mass; $r = 0.07$, $P = 0.78$ for length) or clutch size ($n = 18$, $r = -0.02$, $P = 0.94$). There was no evidence of a trade-off between clutch size and offspring size: hatchlings were no smaller in clutches that were unusually

large relative to maternal body size (testing hatchling mass against residual scores from the regression of clutch size on maternal body length: $n = 18$, $r = 0.11$, $P = 0.65$).

Hatchling sex ratios

Males and females were produced in approximately equal numbers (Table I). The overall mean, based on 18 clutches, was 54% male (S.D. = 18%, range 25–100% male). This mean figure is not significantly different from that expected under the null hypothesis of 50% male (one-sample two-tailed t-test, $t = 0.85$, 1 $d.f.$, $P = 0.41$). Sex ratios in clutches were not significantly correlated with maternal body length ($n = 18$, $r = 0.03$, $P = 0.90$) or clutch size ($n = 18$, $r = 0.01$, $P = 0.97$).

Incubation periods

Reproductive timing was tightly synchronized within the population. Most females laid their eggs in late July, with a range of oviposition dates from 17 to 30 July (Table I). Oviposition date (scored as number of days after 17 July) was independent of maternal body length ($n = 19$, $r = 0.22$, $P = 0.36$), clutch size ($n = 19$, $r = 0.22$, $P = 0.37$) and hatchling mass ($n = 18$, $r = 0.30$, $P = 0.22$). On average, eggs required 35.2 days to hatch (S.D. = 5.19, range = 22–45 days, $n = 18$ clutches). Incubation period was not correlated with mean hatchling size ($n = 17$, $r = 0.30$, $P = 0.24$), clutch size ($n = 18$, $r = 0.11$, $P = 0.65$), or maternal size ($n = 18$, $r = -0.16$, $P = 0.52$). The date of oviposition did not affect the duration of the subsequent incubation period ($n = 18$, $r = 0.01$, $P = 0.98$). However, eggs hatching after a more prolonged incubation produced longer, thinner hatchlings (incubation period versus residual score from the regression of hatchling mass to hatchling length: $n = 17$, $r = -0.61$, $P < 0.009$).
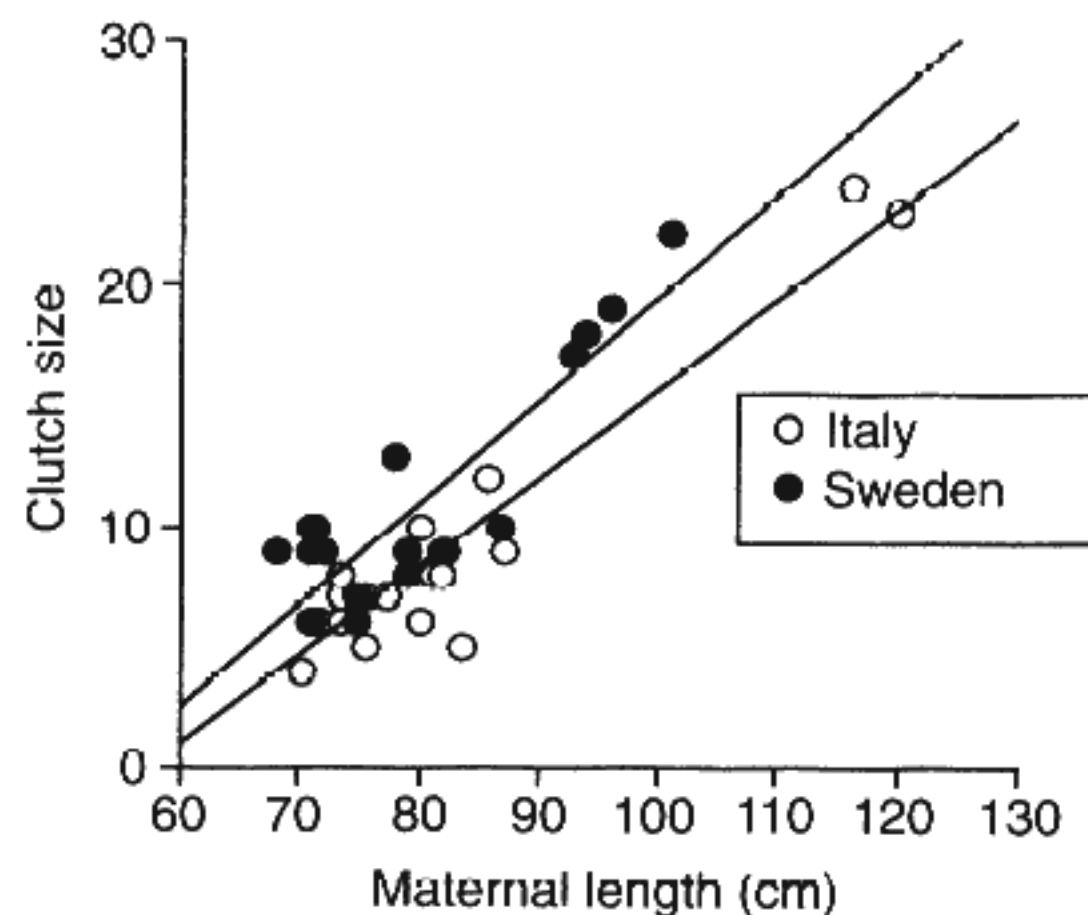

FIG. 2. Clutch sizes increase with maternal body sizes in two populations of grass snakes, *Natrix natrix*, but clutch sizes relative to maternal size are higher in Sweden (●) than in the Carnic Alps of Italy (○). Data for Swedish snakes from Madsen (1983); see text for statistical analyses.

Relative clutch mass

Our female grass snakes produced very large clutches relative to their own body mass. Maternal mass loss at oviposition (RCM) averaged 66% of maternal postoviposition mass (S.D. = 15%, range 35–83%). RCM was not significantly correlated with maternal body size ($n = 16$, $r - 0.33$, $P = 0.22$), mean hatchling mass ($n = 15$, $r = -0.06$, $P = 0.84$), oviposition date ($n = 16$, $r = 0.29$, $P = 0.28$), or clutch size relative to maternal body size ($n = 16$, $r - 0.14$, $P = 0.60$). Similarly, females that were in unusually good body condition prior to oviposition (as judged by residual scores from the regression of maternal pre-oviposition ln mass to body length) did not produce unusually high RCMs ($n = 16$, $r = -0.06$, $P = 0.83$). However, female grass snakes that produced high RCMs were more emaciated after oviposition, presumably as a result of this high expenditure on reproduction (RCM vs. residual score from the regression of maternal post-oviposition ln mass to body length: $n = 16$, $r = -0.69$, $P < 0.004$).

Frequency of reproduction

No female was recorded to produce more than a single clutch within a single summer season, but three females were each recorded to produce clutches in two successive years. All other females were recorded to produce only one clutch of eggs during our study, but may have produced eggs in other years without those clutches being recorded. Hence, records of 'nonreproductive' females in Table I simply mean that we did not record reproduction, not that the female failed to reproduce in that year. Overall, 16 of 18 adult-size females (=19 of 21 records, including records of second clutches for some females) collected in July were gravid at the time of collection, indicating that most females reproduce in most years.

Annual variation in reproductive traits

We used one-factor ANOVA, with year as the factor, to look for any differences among the five years of the study. No such temporal effect was apparent for most of the variables we examined, including offspring size ($F_{3,10} = 1.47$, $P = 0.28$), clutch sex ratio ($F_{3,10} = 0.50$, $P = 0.69$), oviposition date ($F_{3,10} = 1.48$, $P = 0.28$), incubation period ($F_{3,10} = 0.94$, $P = 0.46$), the proportion of inviable eggs ($F_{3,10} = 0.19$, $P = 0.90$), or clutch sizes relative to maternal body sizes ($F_{3,10} = 0.35$, $P = 0.79$). The only trait that differed significantly among years was RCM ($F_{3,10} = 3.74$, $P < 0.05$). The same trend was present (but not significant) for maternal body condition after oviposition ($F_{3,10} = 3.22$, $P = 0.07$).

Dietary habits

We obtained 190 prey items from snakes captured over the period 1987 to 1994, in the study area and in the surrounding region (Table II). Our data reveal significant differences in dietary composition between male and female grass snakes, and significant size-related shifts in dietary habits within both sexes. Adult frogs (*Rana temporaria*) and recently-metamorphosed toads (*Bufo bufo*) are the most common prey types for small grass snakes of both sexes (comparing males < 60 cm to females < 80 cm: $\chi^2 = 6.57$, 4 d.f., $P = 0.16$). Males show a modest (but significant) shift away from this diet as they grow larger, tending to take adult rather than metamorph toads (Table II; $\chi^2 = 16.74$, 4 d.f., $P < 0.002$). However, large females (> 80 cm)

TABLE II

*Prey items recorded from grass snakes, **Natrix natrix**, at Sella Nevea in the Carnic Alps of Italy. These items were regurgitated by snakes after capture. The table provides data separately for male and female snakes. at different ranges of body size (note that females grow much larger than males in this species)*

Prey type	Males		Females	
	< 60 cm	> 60 cm	< 80 cm	> 80 cm
Amphibia: Anura				
Rana temporaria adults	17	19	13	13
metamorphs	6	3	4	0
Bufo bufo adults	0	2	1	21
metamorphs	31	6	23	3
Amphibia: Urodela				
Salamandra atra	1	4	4	2
Triturus alpestris	2	1	6	1
Reptilia: Lacertilia				
Lacerta vivipara	0	0	0	1
Mammalia: Rodentia				
Apodemus sylvaticus	0	0	0	6

take much larger types of prey (especially, adult toads and mice) than do smaller females ($\chi^2 = 45.3$, 6 *d.f.*, $P < 0.0001$) or adult males ($\chi^2 = 25.5$, 6 *d.f.*, $P < 0.0003$).

Discussion

Although our dataset spans five years, the numbers of recaptures of marked snakes (especially during the reproductive season) were much lower than achieved with sympatric smooth snakes (*Coronella austriaca*—Luiselli, Capula & Shine, 1996) or adders (*Vipera berus*—Capula & Luiselli, 1994). The low recapture rate for *N. natrix* reflects the great mobility (very large home ranges) of adult specimens (Madsen, 1984). Thus, some of the null conclusions accepted in our analyses may reflect poor statistical power resulting from low sample sizes. None the less, our work provides the first detailed information for a montane population of grass snakes.

The data reveal both similarities and differences between our population and the two Swedish populations of *N. natrix* for which published data are available. The most extensive data come from studies of grass snakes at Måryd in southern mainland Sweden (Madsen, 1983, 1984, 1987a, b), but information on growth rates and body sizes are also available for a dwarfed island population off the Swedish coast (Madsen & Shine, 1993c). Interestingly, although mean adult body sizes and the size at sexual maturation resemble those of Madsen's (1983) mainland population, growth rates do not. Instead, the Italian snakes grew slowly (Fig. 1), at rates more similar to those of the island population studied by Madsen & Shine (1993c). Hence, maturation was significantly delayed in the montane Italian population of *N. natrix* compared to its lowland Swedish equivalent. Given the extreme phenotypic plasticity in growth rates and adult body sizes in this species (Madsen & Shine 1993c), it seems likely that these differences reflect local climatic conditions, especially the short duration of the growing season each year.

Although our grass snakes resembled those studied by Madsen (1983, 1984, 1987a, b) in their clutch sizes, lack of sexual dimorphism at hatching, and an increase in clutch size with maternal body size, our hatchlings were slightly larger than Madsen's (means of 3.38 g vs. 3 g), and clutch

sizes relative to maternal body sizes were lower in the Italian snakes than in their Swedish conspecifics (Fig. 2: heterogeneity of slopes test $F_{1,31} = 0.60$, $P = 0.44$; analysis of covariance for intercepts $F_{1,32} = 12.23$, $P < 0.002$). This result suggests that there may be a tradeoff between offspring size and clutch size across populations, although our study provided no evidence for such a tradeoff within the Sella Nevea population. Recent work on intraspecific life-history variation in scincid lizards has documented correlated geographic variation in reproductive output and body shape, suggesting that a more heavyset build in females of some populations allows them to increase RCMs (Forsman & Shine, 1996). Given the extensive geographic variation in the morphology of *N. natrix* (Thorpe, 1973), similar divergence in reproductive output may occur within this species also.

One of the most intriguing results to emerge from our analyses was that the body shape of hatchlings (mass relative to length) depended on incubation period, with longer incubation giving rise to longer, thinner hatchlings. This result mirrors recent work on Swedish sand lizards (*Lacerta agilis*), in which genetic factors influence hatchling shape via an effect on incubation periods (Olsson *et al.*, 1996). Presumably, hatchlings that emerge after longer incubation periods are relatively long and thin because they have had more time in which to convert yolk reserves into body tissue (Olsson *et al.*, 1996). Even if such a shape enhances offspring fitness, however, selection may favour early hatching in the cold montane environment at Sella Nevea. The tight synchrony in dates of oviposition (Table I) suggests that delays in oviposition (and hence, hatching) may significantly reduce maternal fitness. Although *N. natrix* probably occupies colder environments than does any other oviparous snake (Arnold & Burton, 1978), and females select the warmest available microclimates for oviposition sites, nest temperatures in unusually cool summers may sometimes be too low for embryonic development to be completed prior to autumn (Smith, 1973). Hence, the population at Sella Nevea may be under strong selection for early hatching. None the less, so long as conditions are warm enough for eggs to develop through to hatching in most years, oviparity may confer a significant benefit over viviparity (Tinkle & Gibbons, 1977). Thus, for example, the reproductive output of *N. natrix* is higher than that of sympatric live-bearers (*Coronella* and *Vipera*) because female grass snakes are able to reproduce annually, with a very high RCM. This high reproductive output may reflect the shorter period during which female grass snakes are burdened with eggs (compared to sympatric live-bearers) and the abundant amphibian prey resource at Sella Nevea. The shift towards larger prey, especially adult toads in larger female grass snakes, mirrors the situation in the Swedish grass snakes studied by Madsen (1983, 1984).

Are there significant 'costs' of reproduction accompanying this high reproductive output in grass snakes? We have no direct evidence of mortality costs, but RCM was correlated with the degree of maternal emaciation after reproduction. The same situation has been reported in two sympatric species of viviparous snakes (*Coronella austriaca* and *Vipera berus*), and in both of these species, a higher degree of maternal emaciation reduced subsequent survival rates (Luiselli, 1992; Luiselli, Capula & Shine, 1996; Madsen & Shine 1993a). This interspecific consistency suggests that RCM may be an important index of three different 'costs': (i) total energy allocation to reproduction; (ii) the degree of physical burdening of the female, and hence her decrement in mobility (Seigel, Huggins & Ford, 1987); and (iii) the risk of starvation of the reproducing female (if, indeed, more emaciated female grass snakes are more likely to die after reproduction). Hence, RCM may offer a convenient and operationally simple measure that broadly integrates costs in different currencies (energy and risk). Further work to investigate the generality of these relationships among snakes would thus be of value.

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