ECOLOGICAL CORRELATES OF REPRODUCTIVE MODE IN REPRODUCTIVELY BIMODAL SNAKES OF THE GENUS CORONELLA

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EVOLUTION OF VIVIPARITY
SNAKES
CORONELLA
SEXUAL SIZE
REPRODUCTION
ACTIVITY
COLD CLIMATE

ABSTRACT – The snake genus Coronella (Colubridae) includes two species, a live-bearing (C. austriaca) and an oviparous taxon (C. girondica). Data were gathered on several life-history traits of both Coronella species in order to shed some light on the selective forces that favoured viviparity, or on subsequent adaptations to the shift in reproductive mode. These data clearly revealed that oviparous and viviparous species are not significantly different in most of the factors that were predicted as favouring the evolution of reptilian live-bearing, including adult body sizes and sexual size dimorphism, offspring sizes, ovulation timing and female frequency of reproduction. Interspecific differences were found in activity patterns, the live-bearing taxon being more heliothermic than the oviparous congener. Moreover, the live-bearing taxon is characterized by its occupancy of colder climates in comparison with the oviparous congener, namely of higher altitudes and latitudes. Our results on Coronella strongly agree with those obtained on the Australian elapid snakes Pseudechis, but falsify several hypotheses on the ecological consequences of the shift in reproductive mode.

ÉVOLUTION DE LA VIVIPARITÉ
SERPENTS
CORONELLA
DIMORPHISME SEXUEL
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CLIMATS FROIDS

RÉSUMÉ – Les serpents du genre Coronella (Colubridae) comprennent deux espèces, C. austriaca, vivipare, et C. girondica, ovipare. Les données proviennent de travaux relatifs à la biologie des deux espèces pour mettre en évidence les forces de sélection qui favorisent la viviparité, ou les adaptations consécutives au changement du mode de reproduction. Ces données montrent que les espèces ovipares et vivipares ne diffèrent pas significativement en ce qui concerne les facteurs prédictifs en vue de favoriser l'évolution des Reptiles ovipares, comme la taille de l'adulte et de la différenciation sexuelle, la taille de la descendance, la fréquence de l'ovulation et de la reproduction. Des différences interspécifiques ont été détectées dans les modes d'activité, les taxons vivipares étant plus héliothermes que leurs congénères ovipares. En outre, les formes vivipares se caractérisent par leur présence dans les régions plus froides que celles occupées par les ovipares, en particulier à plus haute altitude et à des latitudes plus élevées. Nos résultats sur Coronella sont en accord avec ceux portant sur les Serpents australiens elapidae Pseudechis, mais infirment plusieurs hypothèses à propos des conséquences écologiques du changement du mode de reproduction.

INTRODUCTION

Evolution of viviparity (live-bearing, including both "ovoviviparity" and "euviviparity" in this term), being a central feature of reptilian reproductive biology, has been a subject of strong debate among evolutionary ecologists since several decades (Packard et al., 1977; Blackburn, 1982, 1994; Shine, 1985, 1987 a).

According to the general opinion, reptilian viviparity probably derived from oviparity by means of gradual evolutionary processes (Shine and Bull, 1979) and a continuum oviparity-viviparity has been hypothesized (Shine, 1983a; Xavier and Gavaud, 1986). Very recently, some evidence supporting this hypothesis has been found by observing intermediate reproductive characters in the hybrids of oviparous and viviparous Lacerta vivipara (Heulin et al., 1992).

Although many hypotheses on the environmental or species characteristics having important roles in the evolution of viviparity have been proposed, the selective forces favouring this process

are not yet well known (Shine, 1987a). Many reptilian genera, in which both viviparity and oviparity occur, could provide ideal models for comparing closely related species having different reproductive modes (Guillette *et al.*, 1980; Guillette, 1982). According to Shine (1987a), such comparisons may shed light on the evolutionary processes that favoured viviparity or on the subsequent adaptations to the changing reproductive mode.

Amongst the European snakes, the bimodality in the reproductive mode is known in the genus *Vipera* (Viperidae) and in the genus *Coronella* (Colubridae). The former genus is composed by a predominant number of live-bearing taxa, while the latter one by one oviparous (*Coronella girondica*) and one live-bearing (*Coronella austriaca*) species. As for the oviparous taxon, Naulleau (1984, p. 31) hypothesized the occurrence of viviparous populations ("avec tous les intermédiaires possibles entre l' oviparité et l' ovoviviparité"), which, however, have not been discovered up to now.

This paper provides information on the ecological correlates of reproductive mode within the two *Coronella* species.

MATERIALS AND METHODS

This research relies both on bibliography and original data.

Available published data on both *Coronella* species are reviewed, and are discussed where relevant to the predictions analysed in the paper. Additional original information is also given.

Original data on *C. austriaca* were obtained especially from the following three areas :

— (1) Tarvisio Forest (province of Udène Carnic Alps, 900-1100 m a.s.l., north-eastern Italy). This is a mountainous territory characterized by the presence of vast coniferous woods and by typical Alpine climate with rainy spring, cool summer and cold winter with very prolonged snow-covering (Pignatti, 1979). *C. austriaca* is widespread in this area, especially in rocky-stony spots, and at the edges of the coniferous woods. Other snake species are *Vipera berus* and *Natrix natrix*.

— (2) Tolfa mountains (province of Rome, central Italy, 250-500 m a.s.l.). This is a hilly territory characterized by a complex sedimentary basement crossed and overlied by eruptive rocks related to different volcanic cycles. Climate and vegetation are of Mediterranean type (Pignatti, 1979). *C. austriaca* occurs with scattered populations in this area, usually at the edges of *Quercus* and *Fagus* forests. The snake fauna is very diversified. Common species are *Coluber viridiflavus, Elaphe longissima, E. quatuorlineata, Natrix natrix* and *Vipera aspis*.

— (3) Sagittario Valley (Abruzzi, central Apennines, about 800 m a.s.l.). This is a mountainous area with sub-continental climatic characteristics, i.e. with strong seasonal fluctuations, high temperatures and rare rains during summer, cold and prolonged snow covering during winter. In this latter area the smooth snakes were captured in spots belonging to the *Quercetalia pubescentis*. The snake fauna is very diversified. Widespread species are *Coluber viridiflavus, Elaphe longissima, E. quatuorlineata* and *Vipera aspis*.

Data on *C. girondica* were recorded in the territory of Tolfa mountains (see area (2) of *C. austriaca*). In this area *C. girondica* is found only with scattered populations. One of these populations (found in the Rio Fiume Valley, about 300 m a.s.l.) was previously surveyed during the course of an ecological study on this taxon (see Agrimi and Luiselli, 1994, for a description of this locality).

Data on *C. austriaca* from areas (1) and (2) were collected during the course of long-terme studies on ecological strategies of the snakes of these areas (Luiselli and Agrimi, 1991; Luiselli, 1992, 1993; Luiselli and Rugiero, 1993; Capula and Luiselli, 1994 a, 1994 b). Data on *C. austriaca* from study area (3) were collected by one of the authors (LR) during the years 1991-1993.

As proximate environmental factors are known to strongly influence several snake life-history traits, where possible we compared data carried out from the population of *C. girondica* from Tolfa mountains with (1) data carried out from *C. austriaca* populations living in "contiguous parapatry" with the oviparous congener (at about one km each from the other) and under identical climatic conditions, and (2) with data on *C. austriaca* living under different bioclimatic regimes. This could permit us comparisons of some relevance from an ecological point of view.

Statistical analyses were performed by using a SYSTAT computer package, all tests being two tailed. Significance was assessed at a probability level of 0.05. For the choice of the statistical tests, we followed recommendations in Siegel (1956) and in Sokal and Rohlf (1969).

RESULTS

There are many hypotheses about factors important for the evolution of reptilian viviparity, and these hypotheses yield a remarkable array of predictions on ecological characteristics of oviparous versus viviparous congeners.

1. Is reptilian viviparity correlated with harsh climate conditions ?

The principal prediction on the ecological correlates of viviparity in reptiles is that viviparous taxa should occur under climatic conditions different from those of oviparous ones

(colder, hotter, wetter, drier, more unpredictable), as viviparity is an adaptation to increase survivorship of embryos in populations living under harsh conditions (Shine, 1987a). This hypothesis is based on three principal assumptions: (i) pregnant female body temperatures are higher than nest temperatures because of behavioral thermoregulations; (ii) embryonic development is accelerated by this temperature difference; (iii) probability of survival increases in offspring because they hatch before the beginning of autumnal cold (Shine, 1983).

C. austriaca is found both at higher latitudes (Fig. 1 and 2; Arnold and Burton, 1978; Saint Girons, 1982; Rage and Saint Girons, 1990) and at higher elevations than the oviparous congener (Saint Girons 1990a), thus broadly confirming such a prediction. For instance, mountainous populations of *C. austriaca* occur also above 2000 m a.s.l., in the alpine pastures beyond the wooded zone (e.g. in the central Apennines [Du-
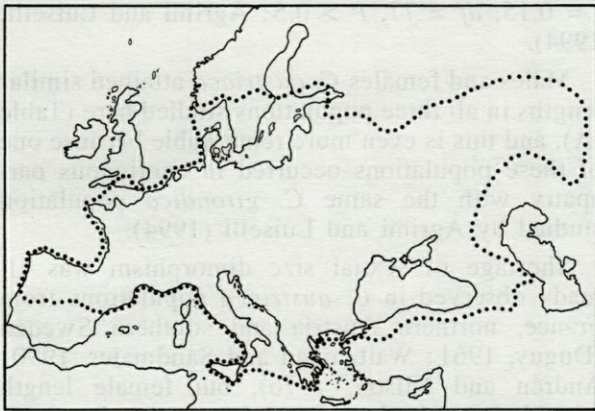

Fig. 1. – European distribution of *Coronella austriaca*.
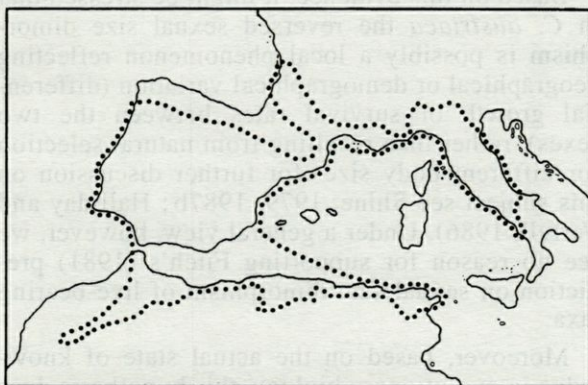

Fig. 2. – European distribution of *Coronella girondica*. Note that this oviparous taxon is found mainly in the Mediterranean region, and that it does not occur in Britain, Scandinavian peninsula, and in other north-European regions where, conversely, its live-bearing congener is actually present.

chessa and Velino mounts, Capula *et al.*, legit] and in the central Alps [Alpe di Siusi, Capula *et al.*, legit]), while *C. girondica* populations do not occur at altitudes higher than 1100 m a.s.l. (Saint Girons 1990b), and are more common at elevations lower than 500 m a.s.l. (Mazzotti and Stagni, 1993; Agrimi, Capula and Luiselli, unpublished).

It is also interesting to note that, when the two species inhabit the same areas, they are never sympatric. In the hilly area of Tolfa mountains, for instance, scattered populations of both taxa inhabit the valley of the stream "Rio Fiume", but the populations of the one species are found at least some hundreds of meters far from those of the other species. Moreover, the two species exhibit different habitat preferences. On the one hand *C. austriaca* inhabits damp-bushy spots bordering the wooded zones (e.g. *Quercus* and *Fagus* forests); on the other hand *C. girondica* inhabits dry pastures with stones and scattered bushes. Though further data are required before stressing firm conclusions, we suspect that such habitat differences may depend on the exigence to reduce interspecific competition between two ecologically similar species (both taxa are similar in body size and dietary habits). In reptile communities, in fact, habitat separation has been shown to be usually the main factor minimizing competition (Pianka, 1966; Jenssen, 1973; Schoener, 1975, 1977), and the distribution of ecologically similar snakes is often complementary (Saint Girons, 1975; 1986).

2. Does body size of viviparous taxa exceed that of oviparous ones?

A second prediction, proposed by Neill (1964), suggests that body sizes should be larger in viviparous than in oviparous species, since females of large species should have less risk of predation than small sized ones during pregnancy.

Adult body size of three *C. austriaca* populations were measured. Data in Table IA reveal that the interpopulation variation in average lengths is small (TL ranging from about 47 to about 52 cm), and that body sizes of these Italian *C. austriaca* are similar to adult body sizes of *C. austriaca* from southern Britain (e.g., see Goddard, 1984). Moreover, contrary to the prediction, adult *C. austriaca* did not differ from adult *C. girondica* in terms of average body length ($P > 0.5$ in all cases).

Gravid females of all *C. austriaca* populations studied here tended to be significantly smaller than gravid females of their oviparous congener ($P < 0.05$-0.01, see Table IB, and compare these data with those given by Spellerberg and Phelps, 1977 and Goddard, 1984, for smooth snakes from southern Britain). Also this occurrence is contrary

Table I. – A, Body sizes (TL, mean ≥ SD, in cm) and sexual dimorphism (analysed by two-tailed Student *t*-test) of three *Coronella austriaca* and one *C. girondica* populations from the Italian peninsula. B, Body sizes (TL, mean ± SD, in cm) of gravid females of three *C. austriaca* and one *C. girondica* populations from the Italian peninsula. All means did not differ at two-tailed Student *t*-test (in all cases, $P > 0.5$). C, Body sizes (TL, mean ± SD, in cm) of offspring *Coronella austriaca* from three study areas of the Italian peninsula.

A

Coronella austriaca

Tolfa Mountains

adult males: $x = 50.72 \pm 3.39$ cm $n = 10$
adult females: $x = 48.94 \pm 4.96$ cm $n = 10$
$t = 0.93$, $df = 18$, $P = 0.362$

Tarvisio Forest

adult males: $x = 51.14 \pm 6.35$ cm $n = 14$
adult females: $x = 48.75 \pm 5.83$ cm $n = 12$
$t = 0.99$, $df = 24$, $P = 0.330$

Sagittario Valley

adult males: $x = 47.36 \pm 4.09$ cm $n = 11$
adult females: $x = 47.30 \pm 3.02$ cm $n = 11$
$t = 0.04$, $df = 20$, $P = 0.960$

Coronella girondica

Tolfa Mountains

adult males: $x = 52.40 \pm 7.89$ cm $n = 42$
adult females: $x = 50.80 \pm 7.50$ cm $n = 37$
$t = 0.15$, $df = 77$, $P > 0.5$

B

Coronella austriaca
Tolfa Mountains: $x = 48.03 \pm 5.20$ cm $n = 8$
Tarvisio Forest: $x = 49.00 \pm 7.37$ cm $n = 7$
Sagittario Valley: $x = 48.28 \pm 2.93$ cm $n = 6$

Coronella girondica
Tolfa Mountains: $x = 56.81 \pm 4.28$ cm $n = 15$

C

Tolfa Mountains: $x = 15.31 \pm 0.85$ cm $n = 39$
Tarvisio Forest: $x = 15.37 \pm 0.83$ cm $n = 30$
Sagittario Valley: $x = 15.27 \pm 1.02$ cm $n = 32$

to the prediction. However, similar findings were already reported for Australian elapid snakes *Pseudechis*, in which females of the viviparous taxon (*P. porphyriacus*) are smaller than females of most of their oviparous congeners (Shine, 1987a).

Maximum body sizes of *Coronella* species is similar : the longest *C. girondica* known measured 86 cm (Duguy, 1960), while *C. austriaca* individuals exceeded sporadically 80 cm (Arnold

and Burton, 1978). With regard to adult body sizes of natural populations of snakes, however, one should remark that they may depend on several proximate factors – e.g. mortality rates, prey availability, duration of the active period due to climatic conditions, etc. – rather than on precise evolutive trends, so that our indications merely seem to represent a tendence.

3. Is sexual size dimorphism more pronounced in viviparous rather than in oviparous taxa?

Fitch (1981) predicted that females should be significantly larger than males in the viviparous species, since the infrequent reproduction of live-bearing females favours increases in body size – and, consequently, in fecundity – at each reproduction.

Sexual size dimorphism was not evident in *C. girondica* from Tolfa mountains, as males ($n = 42$) averaged almost the same total lengths as females ($n = 37$) ($\bar{x} = 52.4 \pm 7.89$ cm vs 50.8 ± 7.50 cm, $t = 0.15$, $df = 77$, $P > 0.5$; Agrimi and Luiselli, 1994).

Males and females *C. austriaca* attained similar lengths in all three populations studied here (Table IA), and this is even more remarkable because one of these populations occurred in contiguous parapatry with the same *C. girondica* population studied by Agrimi and Luiselli (1994).

Shortage of sexual size dimorphism was already observed in *C. austriaca* populations from France, northern Austria and southern Sweden (Duguy, 1961; Waitzmann and Sandmaier, 1990; Andrén and Nilson, 1976), but female length exceeded greatly that of males ($t = 1.98$, $P < 0.05$) in *C. austriaca* from southern Britain (Goddard, 1984).

Based on this evidence, it might be stressed that in *C. austriaca* the reversed sexual size dimorphism is possibly a local phenomenon reflecting geographical or demographical variation (differential growth or survival rates between the two sexes), rather than resulting from natural selection for different body size (for further discussion on this subject see Shine, 1979, 1987b; Halliday and Verrell, 1986). Under a general view, however, we see no reason for supporting Fitch's (1981) prediction on sexual size dimorphism of live-bearing taxa.

Moreover, based on the actual state of knowledge in evolutionary biology, this hypothesis does not appear convincing to us, as it does not take into any account the current theories on the evolution of sexual dimorphism, either under a eco-ethological point of view (relations with the reproductive system – monogamy/polygamy) or under an ecological point of view (intra– / inter-

specific competition). Sexual size dimorphism is often correlated with the occurrence of male combats for access to females during the mating season (Shine, 1978). Males of both *C. girondica* (Agrimi and Luiselli, unpublished observations) and *C. austriaca* (Davis, 1936; Rollinat, 1947) however, are involved in such combats during the reproductive season.

Moreover, sexual size dimorphism may be strongly influenced by, and depend on, differential growth and survivorship rates between the two sexes, rather than resulting from natural selection for different body sizes (Shine, 1979, 1987b; Halliday and Verrell, 1986). Alternative hypotheses also include ecological niche partitioning (Shine, 1980), in which intraspecific competition is reduced by each sex using a different resource (Shine, 1986; Houston and Shine, 1993).

4. Are viviparous taxa more heliothermic than oviparous ones?

Shine (1985) suggested that viviparous taxa should be heliothermic rather than thigmothermic, because oviductal egg retention in cold areas accelerates the embryonic development. Thus, live-bearing taxa should be more heliothermic than their oviparous congeners.

This hypothesis seems to be confirmed by our own observations on *Coronella* species. The oviparous taxon, in fact, spends almost all daylight hours under the stones (about 75 % [n = 141] of *C. girondica* specimens encountered during daylight hours in the territory of Tolfa mountains were under flat stones; for similar findings see also Saint Girons and Saint Girons, 1956; Saint Girons, 1971; Agrimi and Luiselli, 1994), while *C. austriaca* is a diurnal heliotherm, which exhibits precise thermoregulation at relatively high environmental temperatures (> 30 °C) (Gaywood and Spellerberg, 1989).

In this regard it is interesting to note that, though in most live-bearing species the gravid females usually maintain higher body temperatures than non-reproductive females and males for accellerating embryogenesis that is temperature-dependent (Shine, 1980; Beuchat, 1988; Schwarzkopf and Shine, 1991; Capula and Luiselli, 1993, etc.), in other species the gravid females do maintain lower temperatures for avoiding developmental accidents. This is the case of the common lizard, *Lacerta vivipara*, in which the mean body temperature of pregnant females is about 28 °C, while that of males and non-pregnant females is about 30-32 °C (Patterson and Davies, 1978; Heulin, 1987). Also the regression line TC = f (TS) calculated for pregnant females appears to be significantly different from those calculated for males and non-pregnant females (Heulin, 1987).

5. Are offsprings of viviparous taxa larger than those of oviparous ones?

According to a popular hypothesis (Shine, 1978), newborn snakes should be larger in viviparous than in oviparous taxa because higher survivorship of eggs in utero than in the nest may favor an evolutionary increase in size of neonates according to the "safe harbor" hypothesis.

On the one hand, mean body length of *C. girondica* offsprings was about 15 cm (ranging from 12 to 20 cm) in central Italy (Agrimi and Luiselli, 1994), and nearly the same in France (Naulleau, 1984).

On the other hand, *C. austriaca* offsprings averaged about 15 cm in either central or northern Italy (Table IC) and about 13 cm (range = 11/19 cm) in southern Britain (Fig. 4 in Goddard, 1984).

In both species, moreover, offspring mass is usually lower than 4 g (Goddard, 1984; Agrimi and Luiselli, 1994).

Based on these data, no positive support to the "safe harbor" hypothesis has derived, though relatively important interpopulation variations of mean offspring size may possibly occur within the genus *Coronella*.

6. Do ovulation and reproduction timing start earlier in viviparous rather than in oviparous taxa?

A popular hypothesis predicts that the seasonal timing of reproduction may shift, resulting in earlier ovulation in the live-bearing taxon because of the relevant advantages of maternal thermoregulation (Guillette, 1982).

In the territory of Tolfa mountains, where both *Coronella* species inhabit areas with identical climate conditions (see methods), a remarkable similarity between the two species was found to occur. Late May was the earliest period in which ova were detected (by palpation) in the oviducts of potentially pregnant females of both species.

On the other hand, in mountainous areas (Alps and Apennines, where the duration of the snake annual cycle is considerably shortened due to strong extrinsic constraints), first ova were detected at the beginning of June, as in northern latitudes (Goddard and Spellerberg, 1980; Naulleau, 1984).

C. austriaca gave birth from mid-August (Tolfa mountains) to the beginning of September (Tarvisio Forest and Sagittario valley), while *C. girondica* layed eggs in late June, and egg hatched generally at mid August (Agrimi and Luiselli, 1994).

Fecundity parameters of the two species are rather different.

C. girondica was found to produce a low number of eggs ($X = 2.53 \pm 0.83$, $n = 15$, range = 1-4), fecundity and female size (length in cm) being slightly positively correlated (Pearson's $r =$ 0.38, Agrimi and Luiselli, 1994).

C. austriaca was found to produce a higher number of young (Duguy, 1961; Appleby, 1971; Andrén and Nilson, 1976). Clutch size was highly positively correlated to female size (Table II for original data; but see also Duguy, 1961; Spellerberg and Phelps, 1977; Goddard and Spellerberg, 1980; Goddard, 1984, for comparisons). Slopes of regressions relative to all smooth snake populations studied here differed significantly from that relative to *C. girondica* from Tolfa mountains (heterogeneity of slopes test, $P < 0.01$). The reasons for such differences are not completely clear, but it appears rather reasonable that either the scarce correlation between female size and fecundity or the lower number of eggs produced by *C. girondica* depend on its semi-fossorial habits (Agrimi and Luiselli, 1994).

Table II. – Results of regression analysis and ANOVA on the relationships between female size (TL, in cm) and fecundity in three Italian populations of *Coronella austriaca.* For comparison with *C. girondica,* see Agrimi & Luiselli (1994).

Population	Analysis of regression		ANOVA			
	r	r^2	Mean Square	F	df	Signf. P
Tolfa Mountains	.98	96.07%	16.21	146.55	1,8	.00002
Tarvisio Forest	.95	91.20%	14.59	41.45	1,7	.003
Sagittario Valley	.94	89.10%	8.31	32.68	1,6	.004

7. Is there a lower number of clutch per female per year in viviparous females?

According to Fitch (1970), the number of clutches produced per female per year should be lower in live-bearing rather than in oviparous taxa, because of the longer duration of burdening of the female.

Because female frequency of reproduction depends essentially on energy available and remarkable differences are accomplished to local factors (e.g., at higher altitudes or latitudes the female frequency of reproduction is lower than at lower altitudes or latitudes, Saint Girons, 1957; Capula and Luiselli, 1992), the ideal system for testing eventual differences in this reproductive parameter is comparing sympatric or contiguously al-

lopatric populations living under identical or very similar environmental and climatic conditions.

We have exactly done this for stressing our conclusions about *Coronella* snakes from Tolfa mountains.

80% of the female *C. austriaca* ($N = 10$) and about 78% of the female *C. girondica* ($N = 15$) captured in late June were pregnant (differences between the two samples: χ^2 test with $df = 1$ $P > 0.5$). Thus, in both species the female frequency of reproduction appears to be normally annual in Mediterranean environments, and the prediction tested is strongly refused. Moreover, contrary to oviparous lizards such as *Podarcis* species (Barbault and Mou, 1988; Capula *et al.*, 1993), *Coronella* species are unable to reproduce more than once within a season because of insufficient fat body reserves. Also observations carried out in outdoor enclosure support this conclusion.

However, whereas *C. austriaca* was found to mate both in spring and in the early autumn (Luiselli, unpublished observations; Duguy, 1961), the oviparous congener was found to have only a intense spring mating season (Agrimi & Luiselli, 1984).

With regard to the female frequency of reproduction of *C. austriaca,* it must be stressed that this species exhibits annual cycle in central France (Duguy, 1961), and prolonged breeding cycle in more northernly latitudes (e.g. in Sweden and Britain, Andrén and Nilson, 1976; Spellerberg and Phelps, 1977).

Other predictions, for example those proposed by Fitch (1970) and Seigel and Fitch (1984), have not been considered in this note and will be analysed more detailedly in a further paper.

DISCUSSION AND CONCLUSIONS

The overall analysis of the ecological correlates of reproductive mode within the studied snake genus clearly shows that the live-bearing taxon is remarkably similar to the oviparous congener in most of the studied variables that were considered as possible factors stimulating the evolution of viviparity in squamates. Within *Coronella,* in fact, little variation between live-bearing and oviparous species is evident in, e.g., adult body sizes, sexual size dimorphism, reproductive seasonality and hatching sizes. An almost identical result has been obtained by Shine (1987a) in comparing the ecological correlates of reproductive mode within reproductively bimodal Australian snakes of the genus *Pseudechis.* We retain that the similar results obtained by both us and Shine (1987a) are strongly indicative for understanding general patterns in the evolution of reptilian viviparity, be-

cause (1) *Coronella* and *Pseudechis* belong to two distinct phylogenetic lineages (the former is a genus of Colubridae, the latter of Elapidae) and (2) they inhabit very different areas in terms either geographic or environmental.

Most of the hypotheses which have been suggested as factors stimulating live-bearing evolution have not been confirmed by either studies, while only a few predictions have been supported. For instance, the "climate hypothesis" has been supported by both the studies, as live-bearing taxa of either groups inhabit areas much colder than oviparous taxa. However, the prediction that viviparous species should live in unpredictable habitats (Tinkle and Gibbons, 1977) remains rather untestable at the actual state of the knowledge, at least because it is rather difficult to identify the variables for which predictability is to be assessed. If we consider temperatures and precipitations as the more relevant of these variables, we are lead to agree with Shine (1987a) that the results on both *Coronella* and *Pseudechis* are against the above-exposed hypothesis of Tinkle and Gibbons (1977). In fact, these two variables are more predictable at higher than at lower altitudes or latitudes (e.g., see Zammuto and Millar, 1985), so that live-bearing taxa seem to inhabit predictable rather than unpredictable environments. In regard to the "climate hypothesis", we agree with Shine (1987 a, p. 561) that the occupancy of cold climates by live-bearing squamates, though being the most consistent correlate of viviparity within reproductively bimodal reptiles, "could mean either that viviparity has usually evolved in cold climates, or that species in which viviparity has evolved are then likely to invade cold climates".

Another point in which studies on either *Coronella* or *Pseudechis* does agree is in regard to the heliothermicity of the live-bearing taxa. We retain that this characteristic may be a consequence of the shift in the reproductive mode rather than a factor stimulating viviparity, but no definitive proof has been produced in this regard. Thus, we can consider the greater heliothermicity of viviparous species both as cause and as effect of the change in reproductive means. Moreover, although this prediction has been confirmed by the observations on *Coronella,* we are not convinced that most of the viviparous reptiles are more heliothermic than their oviparous congeners.

The theoretical assumption that live-bearing taxa should have a lower number of clutch per female per year than their oviparous congeners has not been supported by our data. However, one should consider that other reptiles with reproductive strategies and parental investment different from these snakes may also verify such a prediction. For instance, Heulin and associates (1994) demonstrated that, because of a second clutch in one year, annual fecundity is higher in lowland oviparous populations than in lowland viviparous populations of the lizard *Lacerta vivipara*. However, the birth dates of viviparous *Lacerta vivipara* populations are similar to the dates at which early eggs of mountainous oviparous populations hatched (Heulin *et al.*, 1991).

At the same time, although some lines of evidence have been found in a few squamate groups (e.g., see Heulin *et al.*, 1992), we do not remain completely convinced that viviparity, which has evolved independently at least 95 times in squamates and in some cases more than once within a single genus (Shine, 1983; 1984), always evolved gradually. The absence of intermediate forms in *Coronella* as well as in numerous other reptile genera with reproductive bimodality, in fact, lead us to think that, at least in some cases, live-bearing might be the result of a relativery rapid and sudden change (e.g., see Eldredge and Gould, 1972; Gould and Eldredge, 1977).

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