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Biogeography of *Lacerta* (*Zootoca*) *vivipara*: reproductive mode and enzyme phenotypes in Bulgaria

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Lacerta (Zootoca) vivipara, has allopatric oviparous and viviparous populations: viviparity is observed from central France and the British Isles to Scandinavia and Russia, while oviparity is restricted to northern Spain and southwestern France, i.e. the extreme southwestern part of the range. Recent observations in the Rila, Balkan, Vitocha, Pirin and Rhodopes mountains indicate that Bulgarian populations of *Lacerta (Zootoca) vivipara* are indeed viviparous. The electrophoretic study of allozymes and the estimation of genetic distances indicate that viviparous lizards from northwest and central France are more closely related to those of Bulgaria, than to the oviparous lizards of southwest France and northwest Spain. Variations in reproductive mode and allozymes are not directly related to geographic distances between populations, nor to their latitude: populations located at the southwest limit of distribution are oviparous and exhibit alleles ATA^{-150} or ATA^{-200}, whereas, at a comparable latitude, the Bulgarian populations are viviparous and exhibit allele ATA^{-100} characteristic of other distant viviparous populations. These findings underline the originality of the oviparous southwestern populations. They do not contradict our previous biogeographic scenario.

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Oviparity is the ancestral reproductive mode of vertebrates (Angelini and Ghiara 1984, Yaron 1985, Wake 1989). Viviparity (live-bearing) has evolved from oviparity (egg-laying) independently in fish, amphibians, reptiles and mammals (Shine 1989). Blackburn (1982), in particular, has demonstrated that viviparity evolved on a minimum of 45 separate occasions in Sauria (lizards). Among current theories on the evolution of viviparity in reptiles the most widely accepted hypotheses suggest that viviparity may be an adaptation to the cold climatic conditions of high latitude and/or high altitude (see review in Fitch 1970, Packard et al. 1977, Tinkle and Gibbons 1977, Shine and Bull 1979, Pilorge and Barbault 1981, Angelini and Ghiara 1984, Shine 1985, Heulin et al. 1991).

Because of the frequent apparition of viviparity in Squamata, one might expect to find key transitional species exhibiting both oviparous and viviparous reproductive modes. Such reproductive bimodality is a very rare phenomenon, reported reliably for only eleven species of lizards and snakes (ten in Shine 1985, more *Lacerta* (*Zootoca*) *vivipara*). Reproductive bimodality has been well documented in the old-world lizard *Lacerta* (*Zootoca*) *vivipara* which has allopatric oviparous (egg-laying + incubation in natura) and viviparous (gestation + parturition) populations (Lantz 1927, Braña 1986, Heulin 1988, 1990).

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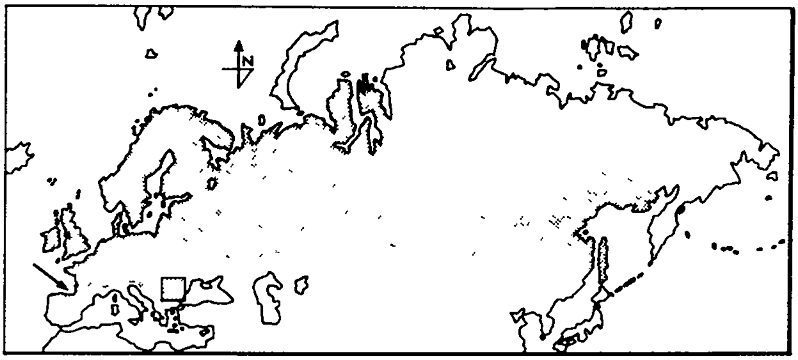
Fig 1 Distribution area of *Lacerta* (*Zootoca*) *vivipara* The arrow indicates the localisation of oviparous populations The square indicates the localisation of Bulgarian populations



Viviparous populations of *Lacerta* (*Zootoca*) *vivipara* are widely distributed from central France and the British Isles to Scandinavia and eastern Russia Oviparous populations are isolated in the extreme southwestern part of the distribution area in the Pyrenees and Aquitaine in southwest France, and in northwest Spain (Figs 1 and 2) (Braña and Bea 1987, Heulin 1989, Heulin and Guillaume 1989)

Characteristics of viviparity (with persistence of non-functional oviparous structures), morphological and ecological resemblances, small genetic distances estimated from electrophoretic analyses, and successful experimental (laboratory) hybridisation all indicate that oviparous and viviparous strains are very closely related (Heulin et al 1989, 1992, 1993, Bea et al 1990, Arrayago et al 1996) This close relationship between the two strains also suggests that the emergence of viviparity is a recent event in this lizard species Previously, we proposed the hypothesis stating that this recent emergence could have occurred during the cold climatic periods of the last quaternary Ice Age In this case, populations (presumably still oviparous) would have retreated in two different directions, to the southwest and southeast Viviparity could have evolved and been rapidly propagated in eastern populations while southwestern populations remained oviparous. After the glaciations, the newly evolved viviparous populations could have (re)colonised northwestern and northeastern countries, without any secondary contact with the residual oviparous populations isolated in the Pyreneo-Iberian refuge areas (Heulin et al 1993) The lack of secondary contact between oviparous and viviparous in France (Figs 1 and 2) could be the consequence of an ecological discontinuity *L* (*Zootoca*) *vivipara* prefers humid biotops (wet heaths, peat bogs) and, because of climatic and edaphic conditions, such biotopes do not exist at present in the geographic area separating oviparous and viviparous populations in southern France (Chouard 1931, Heulin and Guillaume 1989, Heulin et al. 1993).

Our biogeographic hypothesis could well explain the recent evolution of viviparity and the existence of an isolated relictual form, i.e. the oviparous southwestern populations In Bulgaria, *L* (*Zootoca*) *vivipara* is also considered a glacial relic it is restricted to mountain areas (Western and Central Balkans, Vitocha, Rila, Western Rhodopes, Pirin) above 1200 m (Beshkov and Beron 1964, Beshkov 1984) A further interest of these isolated populations is that they are located on the southern limit of the species range, at the same latitude as Pyreneo-Iberic oviparous populations (Fig 1) Because of this geographic symmetry, the original oviparous strain could have retreated and remained unchanged in Bulgaria like in the Pyreneo-Iberian refuge Alternatively, our asymmetric biogeographic scenario suggests that Bulgarian populations of *L* (*Zootoca*) *vivipara* should be viviparous So far, no information has been published on the reproductive mode of the species in Bulgaria For these reasons we

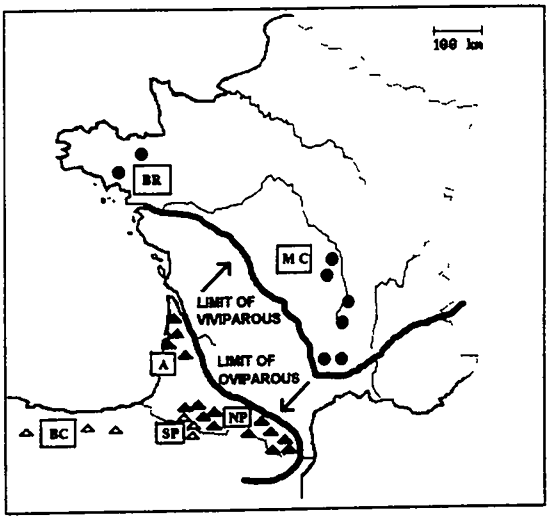


Fig 2 Origins of the oviparous and viviparous samples from Spain and France Open triangles oviparous from the Basque country and Cantabria in NW Spain (BC) and from the south slopes of the Pyrenees (SP) Black triangles oviparous sample from the north slopes of Pyrenees (NP) and from Aquitaine (A) Circles viviparous sample from the Massif central mountains (MC), and Brittany (BR) Approximate northeast limit of oviparous and southwest limit of viviparous (after Heulin 1989)

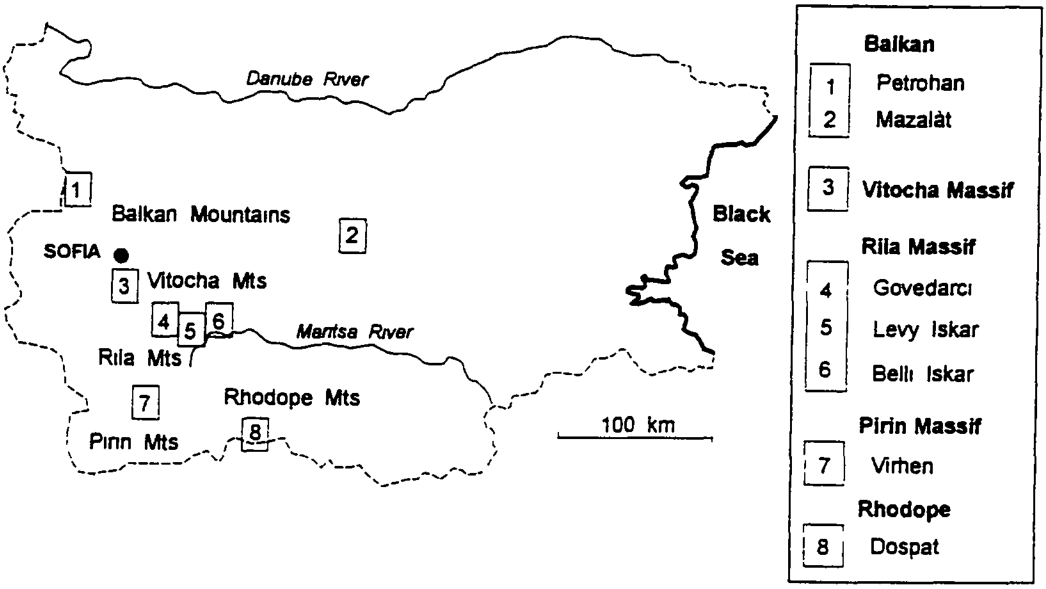


Fig 3 Localisation of the populations of *Lacerta* (*Zootoca*) *vivipara* studied in Bulgaria

set out to study the reproductive mode and the genetic (protein electrophoresis) characteristics of different populations of this species in Bulgaria (Fig 3)

Material and methods

Reproductive mode in Bulgarian populations of *L. vivipara*

We studied the reproductive mode of twenty-three gravid females captured in wild populations (stations 1, 3-7, Fig 3) and kept in laboratory terraria between 15 July and 15 August 1994 eight females from Petrohan (alt 1400-1700 m, lat 43°05′ N, western Balkan), three females from the Vitocha mountain (alt 1850 m, lat 42°40′ N), four females from Govedarci (alt 1300 m, lat 42°10′ N, Rila mountains), two females from Levy-Iskar (alt. 1800 m, Rila), four females from Belli-Iskar (alt 1850 m, Rila), and two females from Vihren (alt 1950 m, lat 41°50′ N, Pirin mountain)

Additional observations on the reproductive mode were available for a population located at Dospat (alt ca 1300 m, lat 41°40′ N, station 2 in Fig. 3) in the western Rhodopes, and for another located at Mazalat (alt ca 1500 m, lat 42°50′ N, station 8 in Fig 3) in the central Balkans (Beshkov unpubl and voucher specimens from the Bulgarian Museum of Natural History)

Electrophoretic comparisons between Bulgarian, French and Spanish lizards

All the animals were captured, transported and put to death with the authorisations of the competent Bulgarian, Spanish and French administrations For the genetic study of Bulgarian lizards, we used nine males and ten females one male and one female from Vitocha, two males and one female from Belli-Iskar, one female from Levy-Iskar, two males and one female from Govedarci, three males and four females from Petrohan, one male and two females from Pirin (Fig 3)

The allozyme characteristics of this Bulgarian sample were compared to those of a viviparous sample from central and northwestern France (20 males, 16 females), and to those of an oviparous sample from southwest France and northwest Spain (36 males, 53 females) The majority of the lizards (77 out of 125) from the two latter samples had been used in a previous electrophoretic study (Bea et al 1990) The oviparous sample consisted of 1) 14 males and 11 females from three localities in the Basque country and Cantabria in NW Spain, (BC populations, lat 42°50′ N, alt 600-1500 m), 2) seven males and 20 females from three localities on the south slopes of the Pyrenees (SP populations, lat 42°50′ N, alt 1100-1900 m), 3) ten males and 19 females from 11 localities on the north slopes of the Pyrenees (NP populations, lat 42°30′-43°5′ N, alt 380-2020 m), 4) four males and three females from four localities in Aquitaine (A populations, lat. 44°-45° N, alt 40-100 m) (Fig. 2) The viviparous sample consisted of 1) 12 males and nine females from six localities in the Massif Central mountains (MC populations, lat 43°40′-46° N, alt 970-1500 m), 2) eight males and seven females from two localities in Brittany (BR populations, lat 48° N, alt 100-150 m) (Fig 2)

Liver and muscle tissues were excised and stored at −30°C awaiting preparation for enzyme extraction. Starch gel electrophoresis techniques (Pasteur et al.

Table 1. Protein trivial names and abbreviations, International code numbers of the Enzyme Commission, number of loci, and electrophoretic systems used. a. Tris-borate-citrate pH 8.7 ("Poulik"), b. Tris-citrate pH 8.0, c. Tris-citrate pH 6.7 with NaDP.

Protein (code)	E.C. No.	N loci	Electrophoretic system
Lactate dehydrogenase (LDH)	1.1.1.27	2	a
Malate dehydrogenase (MDH)	1.1.1.37	1	b
Malic enzyme (ME)	1.1.1.40	1	c
Phosphogluconate dehydrogenase (PGD)	1.1.1.43	1	b
Nucleoside phosphorylase (NP)	2.4.2.1	1	a
Aspartate transaminase (ATA)	2.6.1.1	2	b
Adenylate kinase (AK)	2.7.4.3	1	c
Phosphoglycerate mutase (PGM)	2.7.5.1	1	a
Mannose-phosphate isomerase (MPI)	5.3.1.8	1	c
Glucose-phosphate isomerase (GPI)	5.3.1.9	1	a

1988) were applied to 12 presumed loci (LDH-1, LDH-2, MDH, ME, PGD, NP, ATA$^-$, ATA$^+$, AK, PGM, MPI, GPI) (see Bea et al. 1990) (Table 1).

Factorial analyses of correspondences (FAC) and calculation of genetic distance index (Nei 1972, 1978) were used to compare populations from Bulgaria with the viviparous sample from France, and with the oviparous sample from southwest France and northwest Spain. Because of geographic variations in the allelic frequencies of MPI and NP loci (see Bea et al. 1990), we divided the oviparous sample into two subsets (BC + SP = open triangles and NP + A = black triangles in Fig. 2).

FAC were computed in disjunctive allelic coding with "BIOMECO" software (Lebreton et al. 1990).

Results

Reproductive mode

All the Bulgarian lizards (from all localities) exhibited viviparous reproduction, parturition occurred between 21 July and 8 August and the mean fecundity was six youngs per female (n = 23, SD = 1.7). Moreover, viviparous reproduction had previously been observed in a population located at Dospat (alt. 1300 m, station 2 in Fig. 2) in the western Rhodopes (Beshkov unpubl.), and another was confirmed at Mazalat (station 8 in Fig. 2) from specimens from the Bulgarian Museum of Natural History.

Protein electrophoresis

The relative frequency of alleles are presented in Table 2. From a qualitative point of view, allele ATA^{-100} has previously been observed to be characteristic of viviparous populations from central and western France, whereas alleles ATA^{-150} and ATA^{-200} are characteristic of oviparous populations from southwest France and northwest Spain (Bea et al. 1990). The present study demonstrates that allele ATA^{-100} also is characteristic of the viviparous populations of Bulgaria (Table 2). This result confirms the presence, for the ATA$^-$ locus, of diagnostic alleles separating oviparous from viviparous lizards in all the populations of *L. (Zootoca) vivipara* studied so far.

With regard to the MPI locus, some alleles have been shown to be sex-linked in both viviparous females (MPI^{110}) (Goux and Pasteur 1986, Salvidio et al. 1990) and oviparous females (MPI^{110} for the majority of "French" individuals and MPI^{90} for the others and for all the "Spanish" ones) (Bea et al. 1990). Our results indicate that the same phenomenon exists in viviparous Bulgarian populations.

The projection on the principal plane of the FAC emphasises the importance of loci ATA$^-$ and NP for separating the animals into distinct subsets. Some alleles of loci ME, PGD, and GPI also contribute, to a lesser extent, to separating groups (Fig. 4). At the left of the first axis, we can see oviparous lizards from Spain and the south slopes of the Pyrenees (with ATA^{-150} and ATA^{-200}) while viviparous animals (monomorphous for the ATA^{-100} allele) are at the right. At the left, at the top of the second axis, we find oviparous French and Spanish lizards with allele MPI^{90} and a high frequency of allele NP^{100}, while oviparous French animals with allele MPI^{110} are at the bottom. At the right, viviparous French and Bulgarian lizards (with allele MPI^{110} or MPI^{120}, and higher frequency of allele NP^{150}) are mixed in the centre.

Finally it can be observed that viviparous lizards from Bulgaria are relatively close to viviparous French lizards and distant from other subsets. Furthermore we estimated Nei's genetic distances for all the animals in each subset (Bulgarian viviparous, French viviparous, NP + A oviparous, SP + BC oviparous). These distances (Table 3) also demonstrate that viviparous Bulgarian populations are more similar to viviparous French populations than they are to oviparous ones. The overall Nei's mean genetic distance ($\bar{D}_N$) between viviparous (Bulgarian + French) and oviparous (French + Spanish) lizards is 0.102.

Table 2 Relative frequencies of observed allozymes in *Lacerta* (*Zootoca*) *vivipara* samples Oviparous samples OV1 = from the Basque country and Cantabria (BC) and south slopes of the Pyrenees (SP), OV2 = from the north slopes of the Pyrenees (NP) and from Aquitaine (A) Viviparous samples VF = from France, VB = from Bulgaria

Enzyme locus	Alleles	Oviparous samples			Viviparous samples		
		OV1	OV2	OT (OV1 + OV2)	VF	VB	VT (VF + VB)
ME	90	–	0 04	0 02	0 05	0 16	0 10
	100	0 26	0 22	0 24	0 43	0 50	0 46
	105	0 18	0 12	0 16	0 20	0 08	0 15
	110	0 20	0 27	0 23	0 07	0 18	0 12
	120	0 24	0 24	0 24	0 25	0 08	0 17
	130	0 12	0 11	0 11	–	–	–
PGD	80	0 06	0 03	0 05	0 17	0 03	0 10
	100	0 91	0 64	0 80	0 73	0 97	0 85
	120	0 03	0 33	0 15	0 10	–	0 05
NP	100	0 55	0 76	0 64	0 85	0 39	0 67
	150	0 45	0 24	0 36	0 15	0 61	0 33
ATA$^+$	100	1 00	0 97	0 99	1 00	0 84	0 94
	150	–	0 03	0 01	–	0 16	0 06
ATA$^-$	100	–	–	–	1 00	1 00	1 00
	150	0 42	0 53	0 47	–	–	–
	200	0 58	0 47	0 53	–	–	–
AK	100	0 95	0 84	0 90	0 83	1 00	0 90
	150	–	0 07	0 03	0 17	–	0 10
	200	0 05	0 09	0 07	–	–	–
PGM	60	0 02	–	0 01	–	–	–
	80	0 12	–	0 07	0 02	–	0 01
	100	0 80	0 92	0 85	0 96	0 82	0 91
	120	0 06	0 08	0 07	0 02	0 18	0 08
MPI	90	0 29	–	0 17	–	–	–
	100	0 71	0 70	0 71	0 74	0 71	0 73
	110	–	0 27	0 11	0 19	0 19	0 19
	120	–	0 03	0 01	0 07	0 10	0 08
GPI	60	0 03	–	0 02	0 03	–	0 02
	80	0 12	0 18	0 14	0 09	0 13	0 11
	100	0 85	0 79	0 83	0 88	0 87	0 87
	120	–	0 03	0 01	–	–	–

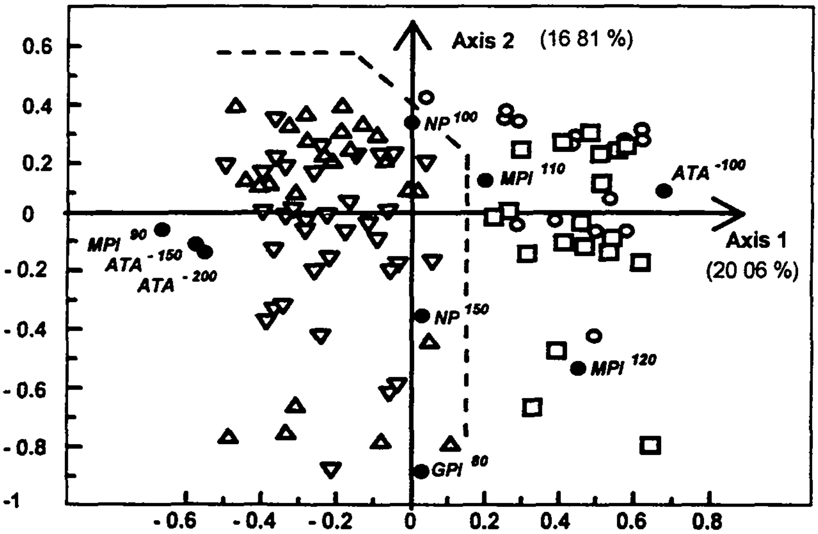


Fig 4 Projection of sampled lizards and of preponderant alleles on the principal plane (axes 1 and 2) of a FAC (factorial analysis of correspondences) (allelic coding) (More than one individual may be plotted in the same place) Squares = viviparous lizards from Bulgaria Open circles = viviparous lizards from France Upward triangles = oviparous lizards from north Pyrenean slope and Aquitaine Downward triangles = oviparous lizards from south Pyrenean slope and from the Basque country and Cantabria Filled circles = position of the preponderant alleles on the two first axes of the FAC Dotted line = separation between oviparous and viviparous populations.

Table 3. Genetic distances (Nei's index, Nei 1978) between the various subsets of oviparous (O) and viviparous (V) populations of *Lacerta* (*Zootoca*) *vivipara*.

	VB	OV1	OV2 (NP + A)	OT (OV1 + OV2)
VF (France BR + MC)	0.056	0.130	0.116	*
VB (Bulgaria St [1] + [3 – > 7])	*	0.121	0.150	*
OV1 (BC + SP)	*	*	0.039	*
VT (VF + VB)	*	*	*	0.102

These small genetic distances are similar, or inferior to distances between subspecies in other Lacertid lizards (Gorman et al. 1975, Guillaume and Lanza 1982).

Discussion

Our studies on the reproductive mode and on the allozyme characteristics indicate that lizards from northwest and central France are more closely related to those of Bulgaria, than they are to the oviparous lizards from southwest France and northwest Spain. On the one hand, the genetic distance between viviparous French and Bulgarian lizards (0.056) is ca half the genetic distance between viviparous and oviparous French lizards (0.102). This clearly contrasts with geographic distances: ca 1700 km between French and Bulgarian viviparous populations, and only 100 km between French oviparous and viviparous populations (i.e. distances between South MC viviparous populations and NP oviparous populations in Fig. 2). Furthermore, our observations also clearly indicate that, despite their proximity to the southern limit of distribution, Bulgarian populations of *L.* (*Zootoca*) *vivipara* are really viviparous.

Finally it can be emphasised that the variations in reproductive mode and allozymes are not directly related to the geographic distances between populations, nor to their latitude. Our study clearly underlines an asymmetrical distribution pattern: populations located at the southwest limit of the range are oviparous and exhibit alleles ATA^{-150} or ATA^{-200} whereas, at a comparable latitude, the Bulgarian populations are viviparous and exhibit allele ATA^{-100} characteristic of other distant viviparous populations. This finding supports, or at least does not contradict, our biogeographic scenario (cf. Introduction) predicting that viviparity could have evolved (first appeared) and been propagated in eastern populations, while oviparity remained unchanged in an isolated southwestern refuge (Heulin et al. 1993). Unfortunately, the location where viviparity first appeared remains unknown. The hypothesis that this evolution could have occurred somewhere between the southern Carpathes and the southern Oural is not excluded. It remains to be studied using genetic comparisons (protein electrophoresis, nuclear and mitochondrial DNA) in a larger number of viviparous populations from the whole distribution area.

To conclude, it seems interesting to compare our results with those of Alcobendas et al. (1996) concerning the Urodele *Salamandra salamandra*. This species also exhibits the same two reproductive modes. Viviparous animals are localised in the Pyrenees and Cantabric mountains (oviparous in lizards), and "[...] the process is complicated by a complex sequence of secondary contacts [...]" between oviparous and viviparous populations resulting in the observation of populations with mixed reproductive mode. Dorsal colour patterns and body size allow the differentiation of large blotched oviparous "subspecies" from small striped viviparous and "mixed" ones (although we are unable to demonstrate any diagnostic morphologic feature between oviparous and viviparous *L.* (*Zootoca*) *vivipara*). Alcobendas et al. (1996), studying the geographic variability in allozymes (34 loci), did not find any diagnostic alleles (whereas ATA^{-} is a diagnostic locus between oviparous and viviparous lizards).

In spite of these differences, for both species 1) the mean genetic distances among populations sampled ($\bar{D}_N$ varying from 0.050 to 0.199 in *S. salamandra* and from 0.039 to 0.150 [Table 3] in *L.* (*Zootoca*) *vivipara*) fall within the intraspecific ranges reported for other comparable animals. Oviparous and viviparous populations are undoubtedly conspecific. 2) There is no direct relationship between genetic distances and geographic distances. Oviparous populations are closer to each other than to viviparous, and conversely. 3) Phylogenetic hypotheses are fairly comparable: viviparity having evolved once in the group and occurring as an intraspecific variation, followed by biogeographical and/or ecological isolation of one form, and radiation of the other, the evolution of the Pyrenean and Cantabric populations being related to the history of glacial activity in the region.

What would occur in oviparous *L.* (*Zootoca*) *vivipara* if a secondary contact with the viviparous took place? *Salamandra salamandra* could be a predictive model as, at present, in Squamata "no single population of any species shows both oviparity and viviparity [...] When a species exhibits both modes of reproduction, the egg-layers and live-bearers inhabit different geographic areas." (Shine 1985).

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