

## Reproductive Tactics of Three *Lacerta vivipara* Populations

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### INTRODUCTION

It may sound like a sophism to say that the study of adaptive strategies requires one to know how environmental factors act upon the life histories of species. However, investigating this comes against a major difficulty, which is to evaluate the relative influence of the various factors involved in the determination of life history strategies.

One way among others that can be used to overcome this obstacle is to consider the variation of the demographic and reproductive characteristics of the same population from one year to another in relation to the fluctuations of environmental factors. Another complementary approach consists in comparing the variability of these parameters between populations of the same species, and relating it to environmental differences. There are now numerous studies documenting such temporal and spatial variation in life histories and population dynamics among lizards /Andrews, 1979; Ballinger, 1973, 1977, 1979 and 1983; Bradshaw, 1971; Dunham, 1981 and 1982; Ferguson, Bohlen and Woolley, 1980; Ferguson and Brockman, 1980; Ferguson, Brown and DeMarco, 1982; Ruby and Dunham, 1984; Snell et al., 1984; Stearns, 1984; Tinkle, 1972; Tinkle and Ballinger, 1972; van Devender, 1982; Vanzolini and Rebouças-Spieker, 1976; Vitt et al., 1978; Worthington, 1982/.

However, most data available on geographic variations in demography and life history characters remain inadequate to test theories of life history evolution. In fact, they are concerned with populations generally very remote from each other. Even the populations of *Sceloporus jarrovi* compared by Ruby and Dunham /1984/ are some 100 km apart. Such distances imply differences in too many factors to enable one to infer any definite conclusion about the mechanisms of limitation and stabilization of the populations. The aim of this work is to reduce the number of sources of environmental differences to a minimum. This is why it deals with three populations living in very similar habitats, and situated at almost the same altitude and latitude in a very short range. This paper presents preliminary results on the demographic and reproductive variation of these populations.

### MATERIAL AND METHODS

*Lacerta vivipara* is a small lacertid lizard, very widespread all over Europe and

northern Asia. It is found in a wide range of rather humid habitats, such as meadows, peatbogs and heathlands, from sea level to 3000 m altitude.

The three populations studied are situated on heathlands mainly composed of *Calluna vulgaris* and *Genista* spp. on the Mont Lozère /France/, at an altitude of 1410-1465 m. Although roughly similar at first glance, the three biotopes show differences in the composition and structure of the vegetation. However, the causal factors of these differences are yet to be elucidated.

The first population, named CMB hereafter, was studied from 1982 onwards. The second one, CCML, is about 12.5 km WNW from CMB in a straight line, and has been studied since 1983. The last one, CPCE, only studied for one year until now, is 2.5 km to the east of CMB.

Densities were estimated using Schumacher-Eschmeyer or Lincoln indices on the basis of mark-recapture data collected in the field. Each lizard, when captured, if not already marked was given a code number by toe-clipping, allowing further identifications. At each capture, the animals were sexed when possible, measured /snout-vent length, total length/ and weighed. The condition of the tail, whether broken or intact, was recorded, and pregnancy was also noted. However, in this paper we only use the snout-vent length data.

Gravid females collected in the field in late June /from CMB only in 1983/ were brought to the laboratory and placed in individual cages. They were regularly weighed until and immediately after parturition. Neonates were counted and weighed immediately after hatching. They were individually marked by toe-clipping only about one week later /to avoid too great a stress at birth/ and then reweighed. Growth in weight - which is not in the scope of this paper - was then regularly measured and the deaths recorded.

Except when otherwise stated all statistical comparisons between samples were made using a t-test.

## RESULTS

### 1. Parturition dates

In 1984, parturition occurred earliest in CCML females, latest in CPCE females /Tab. 1/. A Spearman rank correlation test between the dates of parturition of the three populations shows that CPCE clearly stands out / $r_s = 0.046$  compared with CCML;  $r_s = 0.170$  compared with CMB/, whilst CMB and CCML are more synchronous, though not completely / $r_s = 0.405$ /. The same succession was observed in the field.

Table 1. Parturition dates of the female samples of each population in the laboratory.

	25	26	27	28	29	July		August						
						30	31	1	2	3	4	5	6	7
CCML	3	1	2	3	0	3	2	0	0	1	0	0	0	0
CMB	0	2	1	2	0	3	4	4	0	0	0	0	0	1
CPCE	0	0	1	0	0	1	3	1	4	5	0	0	1	1

2. Average reproductive variables and juvenile survival rates

From the reproductive standpoint, the sample of CCML females statistically differs from the other two /Tab. 2/.

Table 2. Average values of reproductive and survival characteristics in the laboratory for each population sample. N = litter size;  $\bar{w}$  = newborn weight at hatching; SVL = female snout-vent length; W = female body weight after parturition;  $\Delta W$  = total litter weight;  $\Delta W/N$  = individual effort per offspring; S = survival rate;  $\Delta W/W$  = relative clutch mass;  $N\bar{w}/\Delta W$  = weight proportion of offspring in total litter;  $N\bar{w}/W$  = effective reproductive effort.

		CPCE	CMB	CCML
N	$\bar{x}$	4.6 (n=15)	4.1 (n=16)	6.6 (n=15)
	$\sigma$	1.6	1.9	2.3
$\bar{w}$	$\bar{x}$	181.1 (n=65)	180.2 (n=62)	171.7 (n=93)
	$\sigma$	16.2	19.4	18.1
SVL	$\bar{x}$	57.07 (n=15)	55.20 (n=16)	59.60 (n=15)
	$\sigma$	3.39	3.47	3.42
W	$\bar{x}$	3.987 (n=15)	3.783 (n=16)	4.287 (n=15)
	$\sigma$	0.662	0.523	0.580
$\Delta W$	$\bar{x}$	1.69 (n=15)	1.55 (n=15)	2.37 (n=15)
	$\sigma$	0.54	0.50	0.55
$\Delta W/N$	$\bar{x}$	0.384 (n=15)	0.393 (n=15)	0.388 (n=15)
	$\sigma$	0.082	0.142	0.119
S	$\bar{x}$	0.36 (n=65)	0.72 (n=62)	0.27 (n=93)
	$\sigma$	0.41	0.31	0.30
$\Delta W/W$	$\bar{x}$	0.423 (n=15)	0.405 (n=15)	0.559 (n=15)
	$\sigma$	0.109	0.111	0.144
$N\bar{w}/\Delta W$	$\bar{x}$	0.484 (n=15)	0.509 (n=15)	0.467 (n=15)
	$\sigma$	0.097	0.166	0.133
$N\bar{w}/W$	$\bar{x}$	0.204 (n=15)	0.200 (n=15)	0.258 (n=15)
	$\sigma$	0.073	0.070	0.091

As predicted by theory, there is an inverse relationship between the number  $/N/$  and the average size  $/\bar{w}/$  of offspring. CCML females produce substantially more and lighter neonates than do CPCE and CMB females. Moreover, the former have a greater relative clutch mass, and globally invest more energy into offspring than the two others. However, there are no differences between the average reproductive efforts per individual offspring  $/\Delta W/N/$  among the three populations.

With regard to survival rates of newborn young - calculated between birth and October 2, 1984 - CMB neonates have by far the highest average rate, and there is no difference between survival rates of newborn at CPCE and CCML.

### 3. Correlations between the different variables

Although all the possible correlations between all the available variables have been looked for, only those which have a clear ecological meaning are considered in the following discussion.

It is not surprising to find that litter size is positively correlated with female body size - snout-vent length and/or weight. The same holds true for the difference of female weight just before and after parturition  $/\Delta W/$ , but not for relative clutch mass  $/RCM = \Delta W/W/$ . RCM is positively correlated with  $\Delta W$  and with litter size /except for CMB/. However, the "effective RCM"  $/N\bar{w}/W/$  is correlated with SVL only in CMB, and is not correlated with  $W$ . An interesting - and somewhat puzzling - point is the total absence of correlation between the survival rate of newborn young,  $S$ , and all the other variables. There are also few significant correlations between  $\bar{w}$  /average newborn weight at birth/ and the other variables. All the significant correlations are for CPCE, except for the correlation with  $N\bar{w}/\Delta W$  which appears in CCML.

## DISCUSSION

Albeit we lack some crucial information on size and age at sexual maturity, individual growth and mortality rates, we can try to work out and compare some features of the reproductive tactics of these populations. For this purpose, one needs in particular 1/ a knowledge of the true values of the reproductive variables in the field and 2/ a comparison of the reproductive characteristics of equal-sized females /Tab. 3/.

The only variables positively correlated with the body size of reproductive females in the three populations are litter size  $N$ , and total litter mass  $\Delta W$ . When using linear regression equations for both variables in each population to calculate their actual average values /Tab. 3/, it appears that there is no statistical difference with the laboratory result for CPCE, but that CMB and CCML figures have been underestimated in the laboratory samples. However, CPCE and CMB keep very similar average litter sizes and litter masses, still more apart from those of CCML than previously. It is also obvious that these differences are not only due to size differences. The average values of litter size and of total litter mass are still greater in CCML than in the other two populations when comparing females of equal body size /Tab. 3/.

Although slightly smaller than the laboratory estimates /0.352, 0.362 and 0.344 for CPCE, CMB and CCML respectively/, reproductive effort per individual offspring also does not show any statistical difference between the groups.

With respect to the survival rates of the juveniles, the results presented here cannot be considered as very reliable. In fact, it is impossible to be sure that breeding conditions

Table 3. Size-specific values of litter size /N/ and total litter weight /ΔW/ in each of the three populations. Figures in italics correspond to the mean values of each population.  $y_1 = 0.376x - 17.036$ ;  $y_2 = 0.342x - 13.773$ ;  $y_3 = 0.401x - 17.295$ ;  $y_4 = 0.138x - 6.267$ ;  $y_5 = 0.087x - 3.269$ ;  $y_6 = 0.101x - 3.659$ .

SVL \ y = f(x)	N			ΔW (g)		
	CPCE	CMB	CCML	CPCE	CMB	CCML
	y1	y2	y3	y4	y5	y6
55.00	3.66	4.06	4.76	1.32	1.52	1.90
57.61	4.64	4.91	5.80	1.68	1.74	2.16
58.14	4.84	5.08	6.01	1.76	1.79	2.21
60.00	5.54	5.69	6.76	2.01	1.95	2.40
62.00	6.30	6.33	7.56	2.29	2.13	2.60
65.00	7.42	7.31	8.76	2.70	2.39	2.91

were absolutely identical for all neonates: there were differences in the number of young in each cage, and consequently perhaps in the amount of food available to each individual. There were also "dominance behaviours", and perhaps some variability in the physical factors /thickness of the earth layer in the cage, humidity, lighting, heating/ in spite of the care taken to prevent such differences. It would be necessary to evaluate survival in the field by estimating the number of juveniles before hibernation and that of subadults at emergence.

At first sight, with regard to the reproductive characteristics of the three populations in 1984, the CCML population would appear as more r-selected than CMB and CPCE which would look like K-selected populations. Given the apparent global similarity between the three biotopes, one might even suggest a genetic basis to this difference. However, two important points must be taken into account before such conclusions can be inferred.

First, in 1983 the average litter size at CMB was about 6.9 young per female and the average weight of neonates at hatching was 173.7 mg. These values are not very far from those achieved by CCML females in 1984 /7.6 young per female; average weight of neonates = 171.7 mg/! The average body length of reproductive females is estimated at 59.15 mm in 1983, and at 58.14 mm in 1984. In 1984, females of 59.15 mm would have produced 5.4 neonates. Therefore, equal-sized females produced many more offspring in 1983 than in 1984. Even though this interannual difference for the same population is smaller than the interpopulation difference for the same year between CMB and CCML, it is quite important and certainly to be explained, for a great part, by the impact of environmental factors.

Second, instead of remaining deluded by the apparent similarity of the three biotopes, it would certainly be more fruitful to look for the small but perhaps important

differences actually existing between them. Consequently, even if there is a genetic component in the apparently different reproductive tactics of the three populations, environmental factors might also play a great part in the determination of these differences.

A particularly interesting question will be to see whether the reproductive and demographic characters at CCML also fluctuate in the same way as at CMB. In fact, a mean of 7.6 young per female is one of the largest average litter size ever recorded in this species - the other being the average litter size of 7.7 neonates per female estimated by Avery /1975/ - and it seems difficult to imagine it could be still much larger! Therefore, if CCML females produce an approximately constant average litter size from year to year, we should be seeing two very different reproductive tactics: 1/ to produce the greatest possible number of young every year; 2/ to fluctuate when environmental conditions vary. Of course, this is not to be regarded as a definite conclusion to the present work, but better as a working hypothesis for further studies.

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