

DENSITY DEPENDENCE IN THE COMMON LIZARD: DEMOGRAPHIC CONSEQUENCES OF A DENSITY MANIPULATION¹

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Abstract. Density dependence plays an important role in the regulation of most populations. Descriptive studies provide only limited evidence, while density manipulations are thought to be a more powerful tool. Here, we describe such a manipulation.

We experimentally analyzed demographic responses to changes in density in common lizard (*Lacerta vivipara*) populations. Two neighboring sites were studied from 1986 to 1988. At the end of the first year, density was artificially decreased at one site and increased at the other. The evolution of demographic parameters over time (before and after manipulation) was compared between the two sites. We found that: (1) density in each age and sex class quickly converged to pre-experimental values at both sites; (2) survival rates (introduced individuals excluded) were unchanged, except that juvenile mortality was positively related to density; (3) emigration rates remained low and did not seem to be influenced by density, while immigration rates were negatively influenced by density; (4) the proportion of young reproductive females was negatively influenced by density; (5) body length and growth rate were negatively influenced by density only in yearlings, and at least in females, no catchup on growth is apparently possible; no difference in reserve storage was found; and (6) female reproduction was modified by the manipulation through clutch size and hatching success, which were negatively influenced by density; however, no difference was detected for hatching date, number of abortive (clear) eggs, prenatal mortality, reproductive investment, and body mass of live neonates.

Rapid density readjustments were mostly explained by immigration into the site where density was decreased, and by high mortality of introduced individuals and of native juveniles where density was increased. Other parameters that were influenced by the manipulation could only have induced delayed effects on population density.

Different age and sex classes showed different responses to density. These responses indicate that density dependence plays a key role in shaping the demography of this lizard species.

Key words: body size, density; density dependence; density response vs. age and sex; emigration; held experiment, growth; immigration; *Lacerta vivipara*; lizard populations; reproduction; survival.

INTRODUCTION

Population density can be controlled in various ways (Lidicker 1978). Extrinsic factors such as food, habitat suitability, predation, parasitism, environmental fluctuations, or catastrophes are all potential sources of density limitation. Changes in behavioral, physiological, or genetic characteristics with increasing density are also good candidates to explain population regulation (Chitty 1967, Christian 1970, Krebs and Myers 1974, Lidicker 1978, Charnov and Finerty 1980, Eckman 1984). Most likely, population regulation arises from interactions among all of these factors (Hilborn and Stearns 1982, Lidicker 1985, Sinclair 1989). Unfortunately, Charlesworth's (1980) claim that "the full details of the mechanism of regulation of population density have probably never been marked out even for one species" still holds true ten years later.

¹ Manuscript received 15 April 1991; revised 22 November 1991; accepted 15 December 1991; final version received 13 January 1992.

There are numerous difficulties in selecting the principal factors that control population size, and particularly in assessing the role of density dependence: apparent random fluctuation may be produced by overcompensation or delayed density dependence (May 1975, Turchin 1990); apparent density-dependent fluctuations may be induced by autocorrelation in environmental factors (Lebreton 1990, Lebreton and Clobert 1991); the use of inappropriate methods or data often induces the detection of false density dependence or of wrong key factors (Eberhardt 1970, Manly 1977, Lebreton and Clobert 1991). Disentangling these various influences requires long runs of data (Solow and Steele 1990, Sugihara and May 1990).

Some of the difficulties could be overcome:

1) by studying species in which populations fluctuate only moderately. In such cases, density-dependent phenomena are expected to play a major role in shaping the population dynamic, and are more easily detectable. Reptiles appear to be good candidates for this

TABLE 1. Physical traits of sites I and D.

Characteristics	Site D	Site I
Elevation (m)	1410–1420	1420
Slope (%)	2	0
Exposure	South	None
Soil type	Ranker	Ranker
Soil depth (cm)	60–100	60–100
Bed rock	Granite	Granite
Humidity	+++*	++
Area (m ²)	3525	4300
Percentage of the area covered by		
Granite boulders	1	2
Trees >2 m height	10	4
Trees and shrubs <2 m height	60	70
Grasses	50	40
Mosses and lichens	3	1
Dominant plant species†		
Tree >2 m height	Bp and Pu	Pu
Tree and shrub <2 m	Cv	Cv
Grass	Ns	Ns
Number of plant species		
	60	49

* Subjectively, the authors found the humidity greater at site D than at site I.

† Species abbreviations: Bp = *Betula pubescens*; Pu = *Pinus uncinata*; Cv = *Calluna vulgaris*; Ns = *Nardus stricta*.

goal. They show little variation in population size across years (Barbault 1975, Turner 1977, Schoener 1985), and in terms of life history are close enough to birds and mammals, on which most studies of population regulation have been made (Tinkle 1969, Stearns 1984, Dunham et al. 1988). The species chosen here is the common lizard, *Lacerta vivipara*, widely distributed across Europe and Asia, whose population size differs much more between populations than between years within a given population (Bauwens et al. 1987).

2) by manipulating population density. Field experimentation is one of the most powerful tools for investigating animal demography (Krebs 1988), but it raises many problems of design (sample size, replication, etc.: Hurlbert 1984). We chose here to manipulate two populations of 500 animals on two ½-ha sites and to study many parameters over several years. We experimentally increased and decreased density. The scale of the study enabled us to use powerful statistical tools, but prevented us from replicating the experiment. Although density manipulations have been carried out on numerous species (Windberg and Lloyd 1976, Gill 1979, Boonstra and Rodd 1983, Krebs 1985, Semlitsch 1987, Petranka 1989), they have rarely been attempted on this scale, nor have they commonly involved reptiles (Ferguson and Bohlen 1972, Ballinger 1976, Tinkle 1982, Middendorf III 1984). From these studies, the density manipulation should strongly affect one or several life history parameters of our species. However, the magnitude of the effects, the number of responding parameters, and sometimes the direction of the responses are difficult to forecast since current theories

make often contradictory predictions. There is a need here for a general theory capable of handling diverse predictions.

MATERIAL AND METHODS

The species

Lacerta vivipara is a small, live-bearing lacertid lizard (between 50 and 70 mm snout–vent length) inhabiting humid habitats such as peatbogs and heathland. Males emerge from hibernation in late March or April, followed by yearlings and adult females in early May. Mating takes place immediately after female emergence. Parturition usually starts in mid-July and lasts 2–3 wk. On average 5 (range: 1–12) shell-less eggs are laid and hatch soon (from a few minutes to 1 d) after being laid. The activity season ends in late September and juveniles are the last to enter hibernation. A more complete description of life history can be found in Avery (1975), Pilorge (1982, 1987), Pilorge et al. (1983) and Heulin (1985).

Field description and experimental protocol

Three sites were selected on Mont Lozère (Cévennes, France) at an average elevation of 1410 m. They were chosen close to one another (500 m between the most distant points, 25 m between the nearest points) to ensure that all individuals belonged to the same metapopulation. They also showed the locally highest population densities. At one site (D) we decreased the density, at another (I) we increased the density, while the third site (C) was a control. The control site lay between site I and D, closer to I. The areas were as similar as possible in their physical and biological characteristics (Table 1). Unfortunately, at the beginning of the experiment, the introduction of horses near site C induced a large immigration of adults (site I was protected by a band of forest 50 m wide), preventing us from using it as a control plot. Therefore, when a response to the manipulation was detected, it was impossible to attribute this to the density increment (site I) or the density decrement (site D).

The study was conducted from June 1986 to August 1988. The lizards were captured by hand, and individually marked by toe-clipping. The field sites were monitored each year during two experimental periods, June and August. In every such (period), each site was visited several times ($\bar{X} = 9$), with visits evenly distributed over the session duration. The manipulation of density took place at the end of August 1986. We attempted to transfer individuals in proportion to the age and sex structure of sites I and D (Table 2). While this was done successfully for adult (age ≥ 2 yr) males and females (a 100% increase at site I and a 70% decrease at site D, Table 2), we failed to transfer the same percentage of yearlings (a 57% increase at site I and a 55% decrease at site D) due to a lower capture rate. We did not remove juveniles from site D since we could

TABLE 2. Characteristics of the density manipulation of the common lizard, *Lacerta vivipara*, at Cévennes, France.

Lizard category	Decrease site (site D)				Increase site (site I)			
	Initial population		Removals		Initial population		Additions	
	No. inds.	95% CI	No. inds.	% decr.	No. inds.	95% CI	No. inds.	% incr.
Juveniles	491	43–939	0	0	604	0–1224	153	25
Yearlings	163	132–194	90	55	205	165–245	117	57
Adult females	146	115–177	106	73	154	91–217	160	104
Adult males	73	55–91	51	70	109	80–138	109	100
Total*	382	302–462	247	65	468	336–600	386	82

* Calculated without the juveniles.

not decrease their numbers significantly (very low capture rate). We nevertheless introduced 153 juveniles to site I, with an estimated 25% increase in juvenile density. These introduced juveniles were obtained from a laboratory breeding colony mostly originating from the same metapopulation. In all, 539 individuals were transferred, resulting in an overall 82% (juveniles excluded) increase at site I and a 65% decrease at site D (Table 2).

Reproductive parameters were measured by removing and rearing an average of 20 females per year (from mid-July until mid-August) from each site. This removal represents 10% of the female population. After parturition, females with their young were released at their last capture point.

Data and statistical methods

Age, sex, body length and mass, and other morphological and behavioral characteristics were recorded at each capture.

Within each session, captures and recaptures provided data for density estimation. Density estimates were obtained using the computer program CAPTURE (Otis et al. 1978). The methods used in CAPTURE assume a closed population. Nevertheless, the interval between the first and last occasion of capture within a session often exceeded 20 d. Some individuals may have died or moved away during that time and using closed population models for estimating population size might seem irrelevant (Seber 1982). We chose to use them anyway because: (1) the number of captures and recaptures within a session were not large enough to allow estimation of additional parameters (survival rates); (2) mortality is highest just after emergence from hibernation (April and May, Pilorge et al. 1987), i.e., before the beginning of the June session; (3) apparent survival rates (including permanent emigration) from June to August are rarely lower than 85% (Pilorge 1988), which means that apparent survival rate during a session should exceed 95%, indicating a reasonably closed population. A decisive advantage of using CAPTURE is that it provides a means of testing these assumptions.

The apparent survival rate was estimated by recaptures of lizards marked during previous sessions. We used the Cormack-Jolly-Seber model (Cormack 1964,

Jolly 1965, Seber 1965; historical comments in Clobert and Lebreton 1987, 1991) extended to include age effect (Clobert et al. 1987), continuous variable effect (Clobert and Lebreton 1985) and group effect (Pradel et al. 1990, Lebreton et al. 1992) on the survival rate estimation. The computer program SURGE4 (Pradel et al. 1990) was used to fit models including one or several of these extensions and the computer program RELEASE (Burnham et al. 1987) was used to detect problems of heterogeneity (Burnham et al. 1987: TEST 2 and 3). Models were compared by log-likelihood ratio tests (Clobert et al. 1987, Lebreton et al. 1992).

Estimating emigration from the study sites required sampling of the surroundings. Unfortunately, this was only possible in August 1987 for site I and in August 1988 for both sites. No estimation of the emigration rates was possible, but only an instantaneous comparison of the proportion of marked individuals among the individuals caught outside sites I and D.

Unmarked individuals caught in the study areas (either because they escaped capture in previous sessions or because they immigrated) provided the basis for the estimation of the number of immigrants. Jolly (1965) and Seber (1965) designed methods for estimating flows of immigrants into a population. More recently, Nichols and Pollock (1990) and Pollock et al. (1990) have extended these models to discriminate between birth (or change of age class) and true immigration. This method is particularly useful when each capture session is made up of several days (called the "robust design"; Pollock 1982, Pollock et al. 1990). We therefore used Nichols and Pollock's (1990) formula extended for more than two age groups. In order to compare the intensity of immigration between areas, we calculated immigration rates by dividing the number of immigrants from time t to $t + 1$ in one particular age or sex class by the population size of that class at time t . Immigration rate variances were approximated using the standard delta method (Seber 1982). However, the magnitude of the bias introduced by these approximations is unknown. Interpretation of differences among immigration rates must therefore be made with caution.

The age-specific proportion of reproducing females was estimated by dividing the number of mated (exhibiting mating scars) or pregnant females by the total

number of females caught. Age was estimated from size, which is only accurate for juveniles and 1-yr-old individuals. It follows that age of individuals older than one was unknown in 1986.

Average body lengths were compared within each category of sex and age. Differences in body mass or length of an individual captured in two successive sessions form the basis of growth-parameter estimation. Hatching date, clutch size, clutch success (number of abortive eggs, abortive embryos, and stillborn), body mass of live neonates, and female investment were measured from rearing females. For growth and reproduction, statistical methods are outlined in the **Results** section. We used the SPSS/PC+ statistical package (Norusis 1986a, *h*) to carry out these analyses.

For most life history traits, we have information before (June and August 1986) and for two years after the manipulation (June and August in 1987 and 1988). Any response of a particular trait to the manipulation should be exposed as a different trend over the three years in the two sites. We therefore expect a significant interaction between time and site effects on life history characteristics. However, a long-term effect of the manipulation would decrease detection of a significant interaction. Local tests (i.e., each year) should help detect such cases. Most of the comparisons were made using only resident individuals. When sample sizes were too small, transplanted or immigrant individuals were also included if they did not differ from residents. Finally, when site differences were still present in 1988, we looked additionally for their persistence in 1989.

RESULTS

We first evaluated the impact of the density manipulation. Then we investigated factors that may have contributed to a short-term readjustment of density, and finally factors that may have contributed to long-term readjustment.

Density

The computer program CAPTURE provides a selection among eight models for closed populations, which include: (1) time dependence in capture rates (model called $M(t)$), (2) existence of groups of individuals having different capture probabilities ($M(h)$), (3) dependence of capture rates on previous capture history ($M(b)$), and (4) various combinations of these three factors. Among the 36 population sizes that were to be estimated (six sessions \times two sites \times three groups of individuals: males, females, and yearlings), 7 required the simplest model (no time dependence, no group effect, no dependence of capture history), 19 required only model $M(t)$, 7 required other models, and small sample size in 3 cases made density estimation impossible. Capture probabilities are known to be influenced by weather and time of the day in reptile populations (Turner 1977, Pilorge 1988). Among the seven estimates that required a model other than $M(t)$, five

required the model $M(h)$ and two the model $M(bh)$. They were not particular to one year, site, or group of individuals. This suggested that there is some heterogeneity among individual capture probabilities, which could be explained by habitat heterogeneity, differences in activity rhythm, and/or by some border effect. There is probably no handling effect on subsequent captures, as models involving the b effect are rarely found. If the density decrease induced a massive immigration from surrounding populations during the capture sessions, population size at site D could be overestimated. However, this should have induced some heterogeneity among capture rates. Models with an h effect were not selected more often in site D than in site I. We are therefore reasonably confident in the estimates of population size.

Densities of males, females, and yearlings preceding the experiment were similar at the two sites (Fig. 1). The manipulation drastically modified the density in all groups. It was followed by a quick readjustment, which was almost completed by 1988 (Fig. 1). Female densities appeared to be more variable. This is probably related to the different behavior of pregnant females, which move less, and non-pregnant females (in particular post-parturient ones), which move more (Bauwens and Thoen 1981, Heulin 1984, Pilorge 1988).

After the experiment, age structures differed between sites I and D up to August 1987 (Fig. 2), returning to similar values only in 1988.

Survival rate

Estimations of survival rate were based only on individuals first caught in the June and August sessions of 1986 and 1987, except for juveniles for which we also used the 1988 cohort. For each cohort the standard Cormack-Jolly-Seber model satisfactorily described the data for males and yearlings (respectively: $\chi^2_{10} = 16.64$, $P = .681$, $\chi^2_{29} = 35.06$, $P = .203$, TEST 2 + 3: see Burnham et al. [1987] and Lebreton et al. [1992] for further details on this test), except for adult females ($\chi^2_{23} = 35.79$, $P = .040$). After parturition, females wander relatively long distances in search of food (Heulin 1984). Some females are probably only catchable at this time, and this may have induced some capture heterogeneity in August. This is likely to have only a moderate effect on survival comparisons, as this problem was of the same magnitude in the two sites ($\chi^2_6 = 14.55$, $P = .024$, $\chi^2_8 = 17.51$, $P = .021$, for sites D and I, respectively). To increase the power of survival-rate comparisons, we first attempted to reduce the number of parameters (one per field and session) needed to describe capture efficiency. There was a significant variation of capture rates over time in all groups of individuals (log-likelihood ratio tests—males: $\chi^2_6 = 24.54$, $P < .001$; females: $\chi^2_6 = 27.31$, $P < .001$; yearlings: $\chi^2_6 = 27.81$, $P < .001$; juveniles: $\chi^2_8 = 20.68$, $P = .008$). This may be explained by the fact that the number of days to capture (N_c) in each session was not

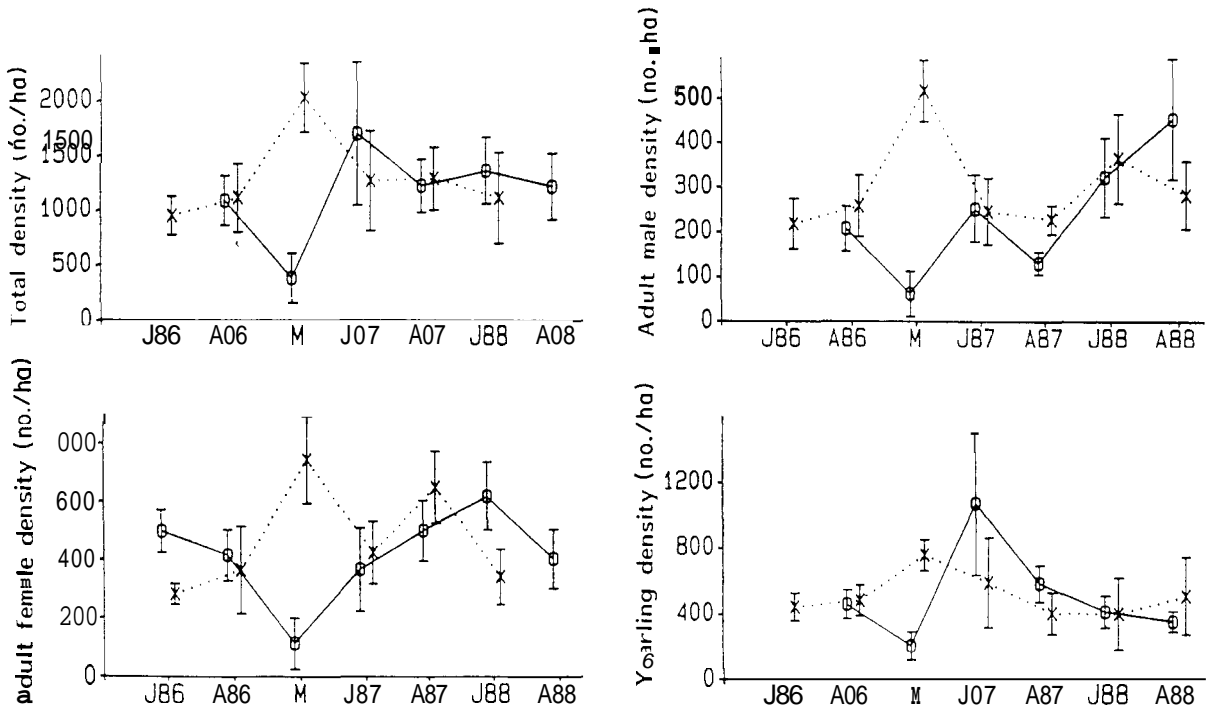


FIG. 1. Densities of the common lizard, *Lacerta vivipara*, at two sites on Mt. Lozere, France, where density manipulations were performed. On the time axis, M = manipulation; J86 = June 1986 session of capture, A86 = August 1986 session of capture, etc.; site D (where lizard numbers were decreased): ○—○, site I (where lizard numbers were increased): × ···· ×; vertical lines = 95% confidence intervals. Density after manipulation was calculated by adding to or subtracting from the number of individuals added or removed.

constant through time. Indeed, N_t satisfactorily described time variation of capture rates for all categories (males: $\chi^2_4 = 8.85$, $P = .065$; females: $\chi^2_4 = 7.96$, $P = .093$; yearlings: $\chi^2_4 = 2.15$, $P = .708$; juveniles: $\chi^2_6 = 6.93$, $P = .328$). The slope of the relationship between N_t and the capture rate was not significantly different between sites (males: $\chi^2_1 < 0.01$, $P = .975$; females: $\chi^2_1 = 1.20$, $P = .274$; yearlings: $\chi^2_1 = 0.86$, $P = .354$; juveniles: $\chi^2_1 = 0.02$, $P = .874$). However, for two categories of individuals, the capture rate was higher in site D than in site I (males: $\chi^2_1 = 2.87$, $P = .090$; females: $\chi^2_1 = 5.29$, $P = .021$; yearlings: $\chi^2_1 = 5.57$, $P = .018$; juveniles: $\chi^2_1 = 2.32$, $P = .128$). To carry on the analysis of survival rate, we kept a model that took into account a systematic difference between the capture rates of sites I and D.

In any year t , individuals first caught in June(t) or first caught in August(t) survived equally well from August(t) to June($t + 1$) and afterwards (males: $\chi^2_{12} = 3.17$, $P = .994$; females: $\chi^2_{12} = 9.82$, $P = .632$; yearlings: $\chi^2_{12} = 9.12$, $P = .693$). Overall, survival rates at site D were not significantly higher than those at site I (males: $\chi^2_5 = 3.77$, $P = .583$; females: $\chi^2_5 = 1.78$, $P = .879$; yearlings: $\chi^2_5 = 3.06$, $P = .691$). At first glance the density manipulation did not seem to have modified survival rates of males, females, and yearlings (Fig. 3). Local tests confirmed this: (1) survival rates

before the manipulation (June–August 1986) at sites D and I were not significantly different (males: $\chi^2_1 = 1.15$, $P = .283$; females: $\chi^2_1 = 0.38$, $P = .535$; yearlings: $\chi^2_1 = 0.22$, $P = .641$); (2) the "winter" 1986–1987

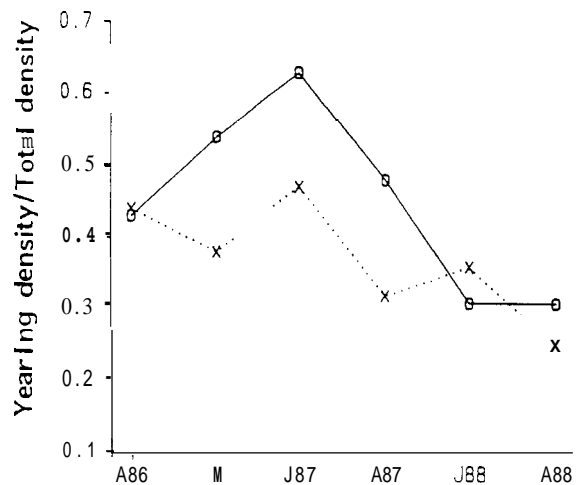


FIG. 2. Yearling-to-total density ratio in *Lacerta vivipara* in sites D (where lizard numbers were decreased, ○—○) and I (where lizard numbers were increased, × ···· ×). June 1986 is not included because of imprecise density estimations. Time axis symbols as in Fig. 1.

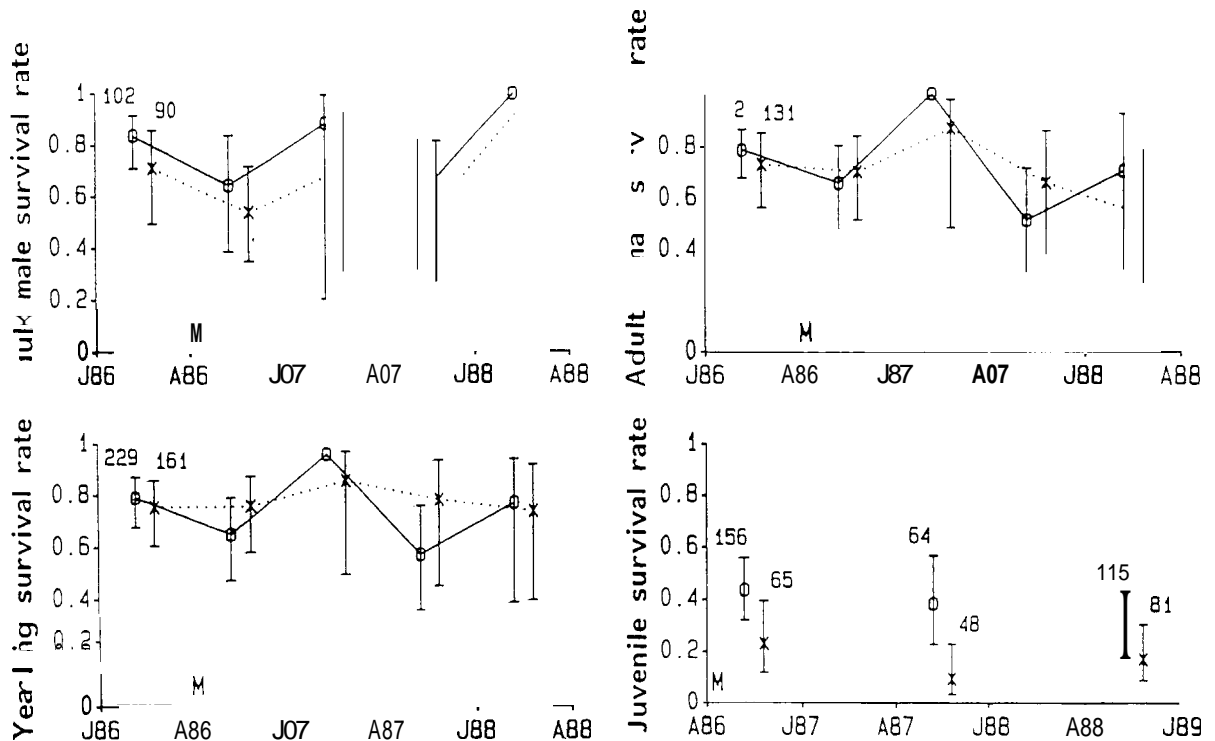


FIG. 3. Survival rates of *Lacerta vivipara* adult males, adult females, and yearlings first caught in 1986, and of juveniles first caught in 1986, 1987, and 1988. Site D (where lizard numbers were decreased): ○—○, site I (where lizard numbers were increased): ×···×; vertical lines = 95% confidence intervals (except for values close to 1 where estimations of variance go to infinity). Cohort sizes are given above confidence intervals. Time axis symbols as in Fig. 1.

survival rate (from August 1986 to June 1987) after the manipulation was apparently not affected (males: $\chi^2_1 = 0.72, P = .198$; females: $\chi^2_1 = 0.07, P = .265$; yearlings $\chi^2_1 = 0.75, P = .193$; one-tailed tests): (3) survival rates in the following summer (June–August 1987) did not differ between sites (males: $\chi^2_2 = 3.18, P = .204$; females: $\chi^2_2 = 0.67, P = .715$; yearlings: $\chi^2_2 = 1.93, P = .381$). The 1986-born juvenile survival rate during winter 1986–1987 and the 1987-born juvenile survival rate during winter 1987–1988 were higher at site D than at site I (respectively $\chi^2_1 = 3.55, P = .030$, one-tailed test; $\chi^2_1 = 5.73, P = .017$; Fig. 3), but the 1988-born juvenile survival rate during winter 1988–1989 was not ($\chi^2_1 = 1.77, P = .183$). Although we lacked a reference point before the manipulation,

we can reasonably conclude that juvenile survival rate was influenced by the density manipulation.

As previously said, transplanted individuals were excluded from the analyses. Their apparent survival rates in site I were significantly lower than those of resident lizards for all categories except juveniles (Table 3).

In summary, the density manipulation did not influence survival rates of the different categories of individuals, except most probably for juveniles. Finally, part of the density readjustment in site I can be explained by the high apparent mortality of transplanted individuals.

Emigration

Individuals outside the two sites were caught in August 1987 and 1988 for site I and in August 1988 for site D. We analyzed only captures > 10 m from the borders. Few individuals seemed to leave sites I and D (5 recaptures out of 50 individuals captured outside site I and 1 out of 19 in August 1987 and 1988, respectively; 1 out of 38 in August 1988 for site D). There were no more emigrants from site I than from site D ($\chi^2_2 = 2.09, P = .176$, one-tailed test), although the date of sampling (1988) might have been a bit late for making this comparison. Furthermore, no individual from site I was recaptured at the control site in spite

TABLE 3. Comparison of survival rates between transplanted and resident lizards in site I (where lizard numbers were increased), just after the manipulation (August 1986 to June 1987). All one-tailed tests.

	Transplanted	Residents	Level of significance
Adult males	0.21	0.51	$\chi^2_1 = 10.24, P = .001$
Adult females	0.31	0.70	$\chi^2_1 = 18.08, P < .001$
Yearlings	0.49	0.75	$\chi^2_1 = 7.02, P = .004$
Juveniles	0.17	0.25	$\chi^2_1 = 0.96, P = .164$

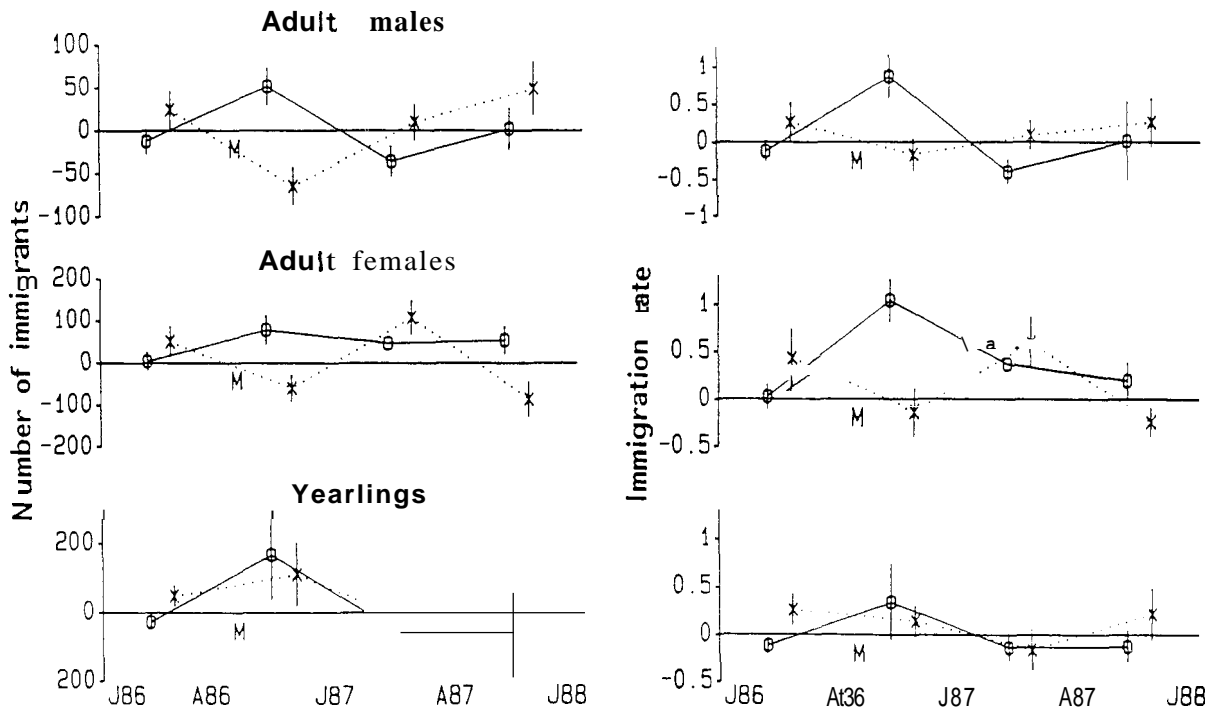


FIG. 4. Numbers of immigrants (left) and immigration rates (right) for *Lacerta vivipara* adult males, adult females, and yearlings. Site D (where lizard numbers were decreased): \circ — \circ , site I (where lizard numbers were increased): \times \times ; vertical lines = \pm 1 SE around the mean. Time axis symbols as in Fig. 1.

of its very close proximity. On the contrary, we found one individual in site I that was initially marked in site C. As far as we can tell, emigration was low from both sites.

Immigration

Before our manipulation, the number of immigrants as well as the immigration rates were higher in site I than in site D for all categories of individuals (from June to August 1986, Fig. 4). From August 1986 to June 1987 it was the opposite. Very few new individuals entered the I population, while strong immigration into site D led to the levelling off of density near its previous value (Figs. 1 and 4). Immigrants likely came from the surroundings, as no transplanted individuals were recaptured at site D. Immigration returned almost to its pre-experiment level by August 1987.

The quick readjustment of density at site D can at least partly be attributed to a substantial immigration of mature animals before June 1987. Immigration into site I was low from August 1986 to June 1987.

Age-specific proportions of breeders

One-year-old females do not reproduce on Mont Lozère. In any year, almost all 3-yr-old (or older) females were pregnant (Bauwens et al. 1987, Pilorge 1988). The proportion of 2-yr-old reproducing females is more variable (Bauwens and Verheyen 1987, Pilorge 1988). As was pointed out in the *Methods* section, we

had no adult females of known age in 1986. However, size is a reasonable estimator of age in young adults. In neighboring populations, most females with a June snout-vent length (SVL) between 45 and 55 mm are 2 yr old (Pilorge 1988). Thus, we analyzed the proportion of reproducing females in this size class, assuming it reasonably describes the behavior of 2-yr-old females.

There were more reproducing females in site I than in D in June 1986 ($\chi^2_1 = 20.71$, $P < .001$, Fig. 5). This difference vanished in 1987 ($\chi^2_1 = 0.13$, $P = .723$, Fig. 5), and reversed in 1988 ($\chi^2_1 = 13.15$, $P < .001$, Fig. 5). This is highlighted by an interaction between year and site ($\chi^2_2 = 41.37$, $P < .001$). The proportion of reproducing females no longer differed between I and D in 1989 ($\chi^2_1 = 0.26$, $P = .610$).

The proportion of reproducing females in this size class was strongly affected by the experiment. This may be because more females were excluded from reproduction in I, or because the average size of 2-yr-old females decreased in I (or increased in D) after the experiment. The second alternative seems unlikely, as 2-yr-old females' SVL were not different between sites in 1987 (Student's $t_{40} = 1.54$, $P = .131$) or 1988 ($t_{39} = 0.74$, $P = .463$).

Body length, growth rate, and body mass

There are fewer data on body mass than on SVL, mainly because we selected only individuals that had

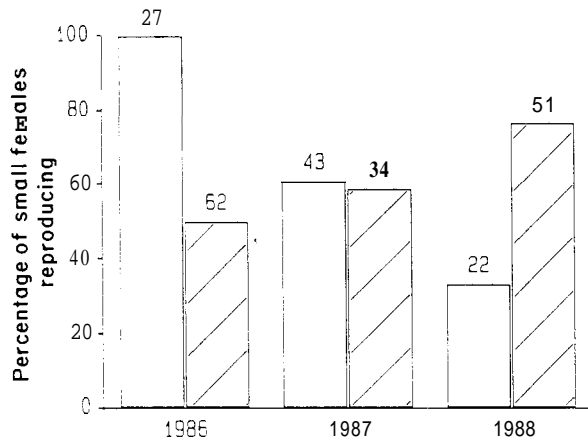


FIG. 5. Proportion of *Lacerta vivipara* small females that were reproducing in June of each year. All these females were 155 mm snout-vent length. Site I (where lizard density was increased): open bars. site D (where lizard density was decreased): hatched bars; sample sizes are given above the bars.

not lost their tail by autotomy. Also, we cannot be entirely sure that all the individuals in 1987 and especially in 1988 had experienced the manipulation (immigrants). Thus, the 1988 sample was restricted to individuals that were present in 1986 or 1987 (and potentially experienced the effect of the manipulation), but this was impossible for yearlings because recaptures of yearlings marked as juveniles were rare.

Body length.—In order to describe the main trends, we first analyzed mean SVL. A three-way ANOVA

with site, period (June, August), and year as factors was performed for males, females, and yearlings.

Adult female body length did not respond to the experiment. No effect of site ($F_{1,952} = 0.82, P = .365$) or of interactions with site (site \times year \times period: $F_{2,952} = 0.74, P = .478$; site \times year: $F_{2,952} = 1.26, P = .284$; site \times period: $F_{1,952} = 1.85, P = .174$) were detected.

Adult males were on average longer at site D than at site I ($F_{1,574} = 18.32, P < .001$; Table 4). This trend did not seem to vary among years or periods (site \times year \times period: $F_{2,574} = 0.24, P = .788$; site \times year: $F_{2,574} = 0.73, P = .483$; site \times period: $F_{1,574} = 0.92, P = .339$).

Differences in mean yearling body length between sites was not constant across years (site \times year \times period: $F_{2,1186} = 2.46, P = .086$; site \times year: $F_{2,1186} = 3.66, P = .026$; site \times period: $F_{1,1186} = 0.33, P = .565$). Yearlings were significantly smaller at site I than at site D both in 1987 and 1988 (Table 4), but not before the experiment. They were still smaller at site I than at site D in 1989 (June: student's $t_{150} = 7.42, P < .001$; August: $t_{150} = 10.69, P < .001$).

Growth rate.—Density affected mean SVL of yearlings. This may suggest a difference in growth rate. Growth rate was estimated on individuals captured in both June and August of the same year (SVL at last capture in August minus SVL at first capture in June divided by the number of days separating the two captures). Growth from August to June can be considered as negligible in our populations (Pilorge 1987), as well as in individuals older than 2 yr. Therefore we excluded

TABLE 4. Snout-vent length (SVL, in millimetres) of adult males, adult females, and yearlings of *Lacerta vivipara* on Mt. Lozère, France, before and after a density manipulation. Lizard density was increased at site I and decreased at site D.

	Before manipulation		After manipulation			
	Jun 1986	Aug 1986	Jun 1987	Aug 1987	Jun 1988	Aug 1988
Adult males						
Mean Site D	51.50	54.18	50.45	53.30	52.54	54.86
Site I	50.45	52.91	49.10	50.44	51.50	53.36
P^*	NS	.039	NS	.002	NS	.032
SD Site D	4.19	3.29	5.20	4.04	4.75	3.13
Site I	4.42	3.11	4.75	4.32	5.26	3.77
P^*	NS	NS	NS	NS	NS	NS
Adult females						
Mean Site D	53.25	56.69	52.97	57.21	54.40	57.04
Site I	53.60	56.29	51.91	56.17	55.77	56.35
P^*	NS	NS	NS	NS	NS	NS
SD Site D	5.06	3.87	5.53	4.99	6.49	3.75
Site I	5.27	4.37	6.13	5.32	5.81	4.40
P^*	NS	NS	NS	NS	NS	NS
Yearlings						
Mean Site D	33.40	41.59	33.89	41.80	35.70	43.50
Site I	32.55	41.23	32.66	38.91	34.22	42.04
P^*	NS	NS	.012	<.001 [†]	.023	.004
SD Site D	4.21	3.82	3.21	2.97	4.02	3.52
Site I	4.69	4.38	3.35	3.97	3.21	3.30
P^*	NS	NS	NS	.006	.070	NS

* P is the probability of no difference between sites I and D (NS for $P > .10$). t test used for comparisons of means and F test used for comparisons of standard deviations (SD). Sample sizes vary between 38 (mostly adults) and 171 (mostly yearlings).
[†] = SVL was square-root transformed to homogenize variance.

this period and these individuals from the analyses. In lizards growing in a logistic way (Schoener and Schoener 1978, Andrews 1982, Pilorge 1988, J. A. Stamps and T. Pilorge. *unpublished manuscript*), growth rate depends on the initial size. In all the analyses the slopes of the relationships between growth rate and initial size (covariance analysis) were not different with respect to sites and years. Growth rates of males, females, and yearlings did not differ between sites I and D before the manipulation (respectively $F_{1,41} = 1.71, P = .199$; $F_{1,55} = 0.21, P = .651$; $F_{1,116} = 0.72, P = .399$). The experiment did not seem to influence growth rate of 2-yr-old adults in 1987 (males: $F_{1,10} = 0.45, P = .518$; females: $F_{1,20} = 0.03, P = .865$), but strongly affected the yearling growth in the way predicted ($F_{1,54} = 9.03, P = .004$, Fig. 6). Growth rate of 2-yr-old adults already resident in 1986 or 1987 were lower in site I than in site D for females ($F_{1,30} = 9.23, P = .005$, Fig. 6), but not for males ($F_{1,15} = 0.50, P = .489$). At least for females, this means that: (1) growth delays cannot be caught up later; and (2) the difference in growth rate persists through time: 2-yr-old females of a given size still showed different growth rates between D and I in 1988. The growth rate of yearlings in 1988 was also higher in D than in I ($F_{1,64} = 4.86, P = .031$, Fig. 6). Not surprisingly, 2-yr-old females in 1989 were smaller in site I than in site D (June: Student's $t_{,} = 2.84, P = .012$; August: $t_{25} = 2.74, P = .011$). However, growth rates of 2-yr-old adults and yearlings were no longer different in 1989 (males: $F_{1,6} = 0.94, P = .371$; females: $F_{1,8} = 0.55, P = .480$; yearlings: $F_{1,54} = 1.02, P = .317$).

Body mass. — The density manipulation could also have affected the way in which individuals gained mass. As variation in adult female body mass is highly dependent on their reproductive status, we will not analyze them. Mass is also strongly correlated with size. For each session, we used the residual values of the relationship between body mass and SVL. The relative gain in mass was estimated by the difference of the residual values between August and June for individuals caught in the same year. Whatever the year and the site, this variable was not related to the number of days separating two captures of a given individual. Variables such as initial or final SVL or difference between final and initial size could influence the relative gain in mass. For each year, covariance analyses with site as a factor and each of these variables as a covariate were performed. No site effect was found. Thus, the relative mass gain was not influenced by the experiment.

Hatching date

Hatching dates were significantly year dependent (analysis of variance with year and site as factors; $F_{2,88} = 5.84, P = .004$). Site effect and site \times year interaction were not significant ($F_{1,88} = 1.09, P = .300, F_{2,88} = 0.48, P = .619$). Hence, the experiment did not modify the hatching dates.

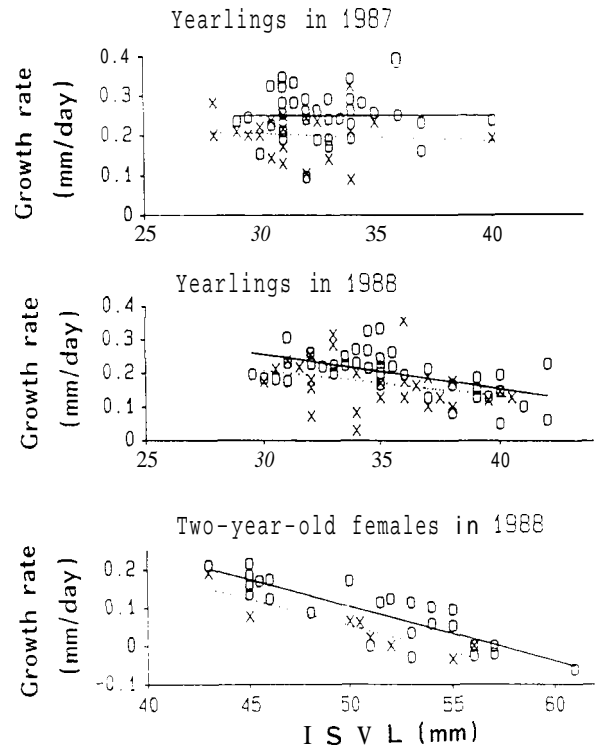


FIG. 6. Relationships between *Lacerta vivipara* growth rate and initial snout-vent length (ISVL) in the cases where the slopes of these relationships at sites D (where lizard numbers were decreased, \circ — \circ) and I (where lizard numbers were increased, \times — \times) were significantly different at $\alpha < .10$.

Clutch size

In many reptiles, clutch size is directly related to female body length (Avery 1975, Barbault 1975, Turner 1977, Pilorge et al. 1983, Heulin 1985). Therefore, we performed covariance analyses with clutch size as the dependent variable, female body length as the covariate, and site as a factor. These analyses showed that (Fig. 7): (1) the relationship between clutch size and female body length did not differ between sites in 1986 (site effect: $F_{1,24} = 0.74, P = .398$; equality of slopes: $F_{1,23} = 0.08, P = .785$); (2) females at site D produced more eggs than females of similar size at site I in 1987 (site effect: $F_{1,37} = 4.05, P = .052$; equality of slopes: $F_{1,36} = 2.17, P = .150$); and (3) this difference was still present in 1988 (site effect: $F_{1,37} = 5.61, P = .023$; equality of slopes: $F_{1,36} = 0.64, P = .430$). By 1989, clutch size of females was no longer different between sites (site effect: $F_{1,74} = 0.16, P = .694$; equality of slopes: $F_{,} = 1.96, P = .165$). Thus, population density had some influence on clutch size even when female body length was taken into account.

Clutch success

The proportions of within-clutch losses did not differ between sites in 1986 and 1988 (respectively $\chi^2_1 < 0.01, P = .974$; $\chi^2_1 = 1.02, P = .313$; Fig. 8). Egg and

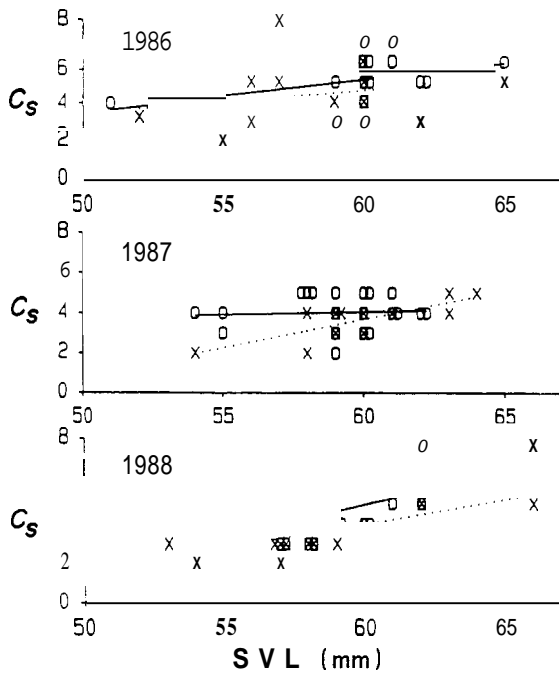


FIG. 7. Relationships between clutch size (C_s) and female snout-vent length (SVL) of *Lacerta vivipara* in sites D (where lizard numbers were decreased, \circ — \circ) and I (where lizard numbers were increased, \times ... \times).

hatchling mortality was higher in site I than in site D in 1987 ($\chi^2_1 = 4.48, P = .017$, one-tailed test). The number of clear and abortive eggs, probably reflecting the quality of egg production and fertilization, and the number of abortive embryos, assumed to depend on the quality of the egg environment during early development, did not vary significantly across years and sites (respectively $\chi^2_2 = 4.45, P = .108$; $\chi^2_2 = 0.95, P = .330$). The higher clutch losses in 1987 at site I were better explained by the higher number of stillborn offspring ($F_{1,35} = 3.79, P = .026$, one-tailed test, Fig. 8). The latter offspring were significantly lighter than live young ($F_{1,35} = 9.17, P = .003$). This may indicate that (1) some young were unable to use the yolk reserves efficiently before hatching; (2) exchanges of water and minerals between mother and eggs varied within clutch; and (3) females might not invest the same amount of energy reserves into each egg.

Body mass of live neonates

We analyzed only the mass of the young. Inaccuracy of body length measurement in juveniles was too large to be distinguished from true natural variability. Possible sex differences in body mass at birth (Pilorge 1988) were not taken into account. However, a recent study showed that the sex ratio at birth was not significantly site dependent (J. Lecomte, *personal communication*).

In every site and year, 75% to 90% of the variation of juvenile body mass was explained by variability

among litters. Therefore, the mean body mass of live young in each clutch was used instead of individual hatching mass, as each hatchling could not be taken as an independent point.

Hatching mass did not seem to vary across years and sites. However, juvenile body mass may depend on both female body length and clutch size (although see Bauwens and Verheyen 1987). A covariance analysis confirmed this (female body length: $F_{1,77} = 19.27, P < .001$, and clutch size: $F_{1,77} = 20.49, P < .001$). When these effects were accounted for, no remaining variation was found to be significant (year effect: $F_{2,77} = 2.49, P = .089$; site effect: $F_{1,77} = 0.53, P = .471$; and, more importantly, site \times year interaction: $F_{2,77} = 1.63, P = .202$).

In conclusion, the body mass of successfully hatched young was not influenced directly by the experiment.

Female investment

Females of a given SVL had a smaller clutch size and proportion of live young in site I than in site D just after the density manipulation. Did those females invest differently in reproduction? To investigate this issue, we estimated the relative clutch mass (RCM: [clutch mass] divided by [female body mass before parturition]). ANOVA with site and year as factors showed that RCM varied significantly across years ($F_{2,92} = 5.47, P = .006$), and between sites ($F_{1,92} = 10.49, P = .002$). No interaction between sites and years ($F_{2,92} = 1.13, P = .328$) was detected. However, local tests

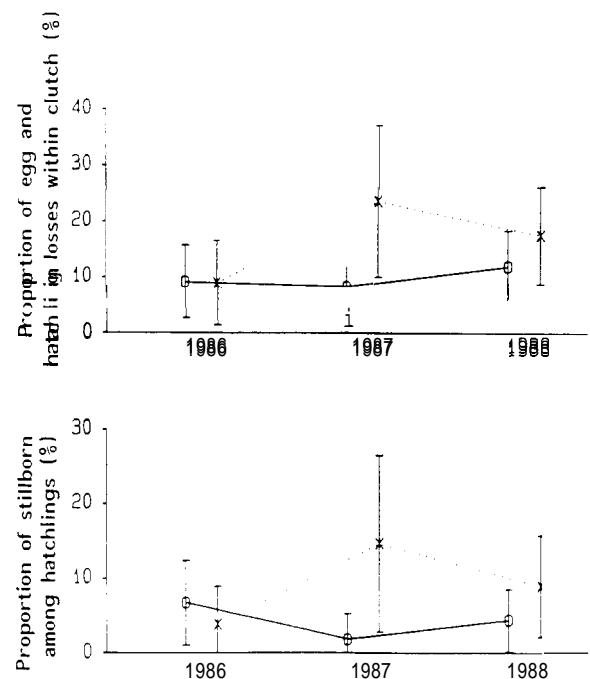


FIG. 8. Clutch success of *Lacerta vivipara* in sites D (where lizard numbers were decreased, \circ — \circ) and I (where lizard numbers were increased, \times ... \times). Vertical lines = 95% confidence intervals.

indicate a lower RCM at site I than at site D in 1986 (Student's $t_{25} = 2.24$, $P = .034$) and in 1987 ($t_{22} = 2.80$, $P = .011$), but not in 1988 ($t_{40} = 1.06$, $P = .294$; Fig. 9). Overall, although their reproductive success after the manipulation was low, females in site I did not invest differently in their reproduction than females in site D.

DISCUSSION

General comments

Replications of ecological experiments in natural conditions are often lacking (Hurlbert 1984), mainly because the necessary investment in money and effort places them out of reach for many ecologists. Consequently, a treatment effect, for example, cannot be separated from a site effect. This work does not escape from this criticism. Fortunately, the species under study showed few differences across sites in most of its life history traits before the experiment. In addition, most of these parameters converged towards the same values 1–3 yr after the manipulation, which increased our confidence in the way we interpreted the dynamics of our populations during the experiment. Ultimately, the generality of our conclusions will be determined by comparison with similar studies (Lebreton and Clobert 1991).

A first result of this work is the quick readjustment of total density in the two manipulated sites. This quick readjustment was expected, as the populations were open (Krebs 1988). This probably limits the generality of our conclusions—in particular for those parameters that were not affected by the experiment. Be that as it may, this experiment shows the ability of populations of the common lizard to regulate their density in such open systems. However, our study sites were not random subsets of an evenly populated area. The two areas were chosen because of their high density. They were probably the most attractive for lizards. Thus, it was a priori unlikely that surrounding populations would completely overshadow the impact of the experiment.

A large number of life history traits were modified by the change in density. Obviously, not all of them played the same role in the quick readjustment of the density we observed. Indeed, as the experiment was conducted at the end of the activity season, variations in survival rate, emigration and immigration could directly influence the population density the next year, while variation in other traits such as growth rate, fecundity, or age-specific proportion of breeders could only have a longer term effect.

Life history traits inducing a short-term effect on population density

As expected for an open population, immigration of individuals from surrounding populations played the key role in the readjustment of density at site D. Immigration brought the total density back almost to its

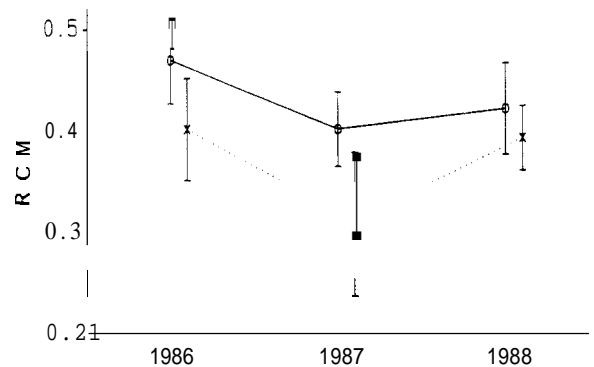


FIG. 9. Relative clutch mass (RCM) of *Lacerta vivipara* in sites D (where lizard numbers were decreased, \circ — \circ) and I (where lizard numbers were increased, \times ... \times). Vertical lines = 95% confidence intervals.

pre-experiment value by June 1987. However, in spite of this quick readjustment, age structure remained modified until August 1987. Surprisingly, emigration did not seem to play a role in the density readjustment in site I. This may indicate that the common lizard behaved like species that favor philopatry over dispersal in situations of high population density (habitat saturation model; Smith and Ivins 1983, Jones et al. 1988).

Survival rates of resident (non-manipulated) males, females, and yearlings were density independent and did not contribute to density readjustment. The high apparent mortality of introduced individuals contributed most to density readjustment at site I, and immigration to the density readjustment at site D.

In addition, local recruitment (juveniles entering the yearling class) was density dependent, as juvenile survival rate was very different between the two sites in 1986 and 1987, but not in 1988. However, our loss of the control site prevented us from defining the precise role of juvenile survival in the density readjustment.

Life history traits inducing a long-term effect on population density

Although total density on the two sites returned to its previous level as soon as June 1987, fecundity parameters as well as growth rates remained affected by the manipulation. However, the experiment modified the age structure of the population. At site I, yearlings were relatively less abundant as local recruitment was low (poor juvenile survival from August 1986 to June 1987). This maintained an overrepresentation of reproductive individuals in 1987 and, in consequence, a higher rate of social interactions in that population than at site D (J. Lecomte, *personal communication*).

Unfortunately, the lack of a control site once more prevents us from ascribing a change in one trait to a positive or negative change in density. We can say, however, that: (1) the proportion of small reproducing females (mostly 2-yr-old females) was negatively influ-

enced by density, but not through a modification of body length in either 1987 or 1988; (2) clutch size (corrected for body length) and hatching success were negatively density dependent; and (3) growth rate of yearlings was negatively related to density. At least in 2-yr-old females, the delay in growth was not compensated for later on.

All these factors led to a substantial modification in the local reproductive rate (site I: 2.47 births/female; site D: 3.93 births/female), and in the short-term local recruitment rate (I: 0.26; D: 1.58). Differences in future adult female body length (associated with a difference in clutch size) should act in the same way, but over a longer period of time.

Sensitivity of the different age and sex classes to density

Different parameters responded to the manipulation according to sex and age. Adult males were not noticeably affected by the experiment. Adult females (≥ 2 yr old) were only affected in their current reproduction (proportion of small-sized females that reproduced, clutch size, and hatching success). In 1987 their current and future survival rates were not modified by the density manipulation, nor were their growth rates and energy reserves. They did not seem to endanger their potential future reproductive success. Unfortunately, we could not measure the realized future reproductive success, because the 1987 and 1988 reproductive traits were known for a given female in just a few cases. The above findings are not direct evidence of a tactic implying the existence of a cost of reproduction (Reznik 1985). Density-independent (or slightly dependent) adult survival could be a general feature of reptile demography (Laurie and Brown 1990a). However, the existence of a cost of reproduction expressed through growth and survival was recently demonstrated in a reptile (Laurie 1990, Laurie and Brown 1990a). The present results are consistent with a tactic whereby females sacrifice current reproductive success in order to maintain future reproductive opportunities.

Juveniles born in 1986 or 1987 in site I survived less well than those born in site D. Juvenile survival rates, unlike those of adults, were density dependent. Similar results have been found in other studies (Swingland and Coe 1979, Laurie and Brown 1990). In 1987, survival rates of individuals born in 1986 no longer differed between sites, but their growth rate and final size were strongly affected by density, as found in amphibians (for example, Scott 1990). This size effect may change their future reproductive success (Sinervo 1990), directly through their future reproductive performance (Sinervo and Huey 1990), but also indirectly through their future social status (Stamps 1988). As juvenile density was not noticeably modified, only the existence of asymmetric competition or interference from older individuals can explain these results. There may be competition for shelter or basking sites as well

as for food, as the overlap in size of food items between juveniles and older individuals is significant (Heulin 1984).

More generally, interaction between sexes and ages was thought to be asymmetric in this species, adult males successfully competing with adult females, while both are dominant over yearlings (Pilorge et al. 1987, Pilorge 1988). Although our experiment was not designed to study asymmetric competition (Krebs 1988), we showed that each class of individuals was affected in different life history traits: juveniles in their survival rate, yearlings in their growth, females in their reproduction, and males in no obvious way. This confirmed that density does not have the same effect with respect to age and sex (Begon 1984, Clobert et al. 1988, Laurie and Brown 1990a).

Some implications for population dynamics of the common lizard

In the common lizard, most of the life history traits are much more variable between populations than within populations over time (Bauwens et al. 1987). This variation is mainly due to differences in female body size that result in differences in age at first reproduction and in clutch size (Bauwens et al. 1987, Pilorge 1988), and to differences in juvenile mortality rate. Biotic factors such as predation have been proposed to explain these differences (Bauwens et al. 1987, Pilorge 1988), and density dependence is thought to shape the life history traits. Our experiment confirmed the key role of density dependence. Juveniles' mortality responded to a change in density. Their growth rate immediately following the manipulation, and more importantly their growth rate as 2-yr-olds, were also modified. This suggests that, at least for females, competition occurring at an early age is sufficient to produce small adults. No recovery in size is apparently possible, supporting general predictions that "catching up" growth is not necessarily an optimal strategy for "retarded" individuals (Sibly and Calow 1986). Individuals suffering a delay in growth may prefer to save part of their future reproductive success by maturing reproductive organs or finding a site for reproduction, rather than diverting energy to grow faster or longer and, as a consequence, delaying the age at which they mature. As expected, clutch size (body size effect removed) and hatching success were also density dependent. However, the body mass of the live-born young was not density dependent when corrected for female body size and clutch size. At site I, females produced young of the same mass, but in smaller numbers (the same result was found in a snake, Ford and Seigel 1989). This tactic confirms that size at birth is an important determinant of fitness of young in *Lacerta vivipara*, as generally in reptiles, both for future survival and final adult size (Ferguson and Fox 1984, Sinervo 1990). This also has important implications for demography, since even under conditions of high intra-

specific competition during gestation, young seem to be able to become large adults

ACKNOWLEDGMENTS

We are grateful to D. Bauwens, E. Danchin, R. Ferrière, D. Promislow, and T. W. Schoener for very constructive criticisms on an earlier draft of this paper. Many valuable suggestions and comments were also made by P. Waser, J. Nichols, and an anonymous reviewer. We also thank all the people who helped in collecting data, and the Office National des Forêts and the Parc National des Cévennes for providing very good conditions for work in the field. The French Ministère de l'Environnement financially supported this study (grant S.R.E.T.I.E. 87352).

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