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Variation of reproductive traits in a population of the lizard Lacerta vivipara

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Variation in reproductive traits (sexual maturity, clutch size, clutch weight, mean egg mass, newborn weight) was studied during a four year period in a population of the live-bearing lizard *Lacerta vivipara*. Sexual maturity was associated with attaining a minimum body size. Clutch size increased with female body length and litter weight increased with clutch size. A major component of the within year variation in these reproductive traits was attributable to female size. Analysis of successive clutches in individual females indicated that a significant fraction of the variation in litter size adjusted for female length, was due to consistent differences between individuals. Newborn weight varied within and among litters, but no relations between hatchling mass or mean egg mass in a litter and other traits were detected

Size-adjusted reproductive performances remained constant during the course of this study, even though environmental conditions (weather factors, food availability) varied annually. Observed among year variations in reproductive characteristics were attributable to differences in the body size distributions of the adult females.

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1. Introduction

Lizard life histories have received considerable attention in recent years. Numerous thorough studies have documented variations in life-history traits between species (e g. Tinkle 1969, Tinkle et al. 1970, Ballinger 1973, Vitt and Congdon 1978, Dunham 1981) as well as among populations of single species (e g. Pianka 1970, Tinkle and Ballinger 1972, Dunham 1978, 1982, Van Devender 1978, Schoener and Schoener 1978, Ballinger 1979, 1983, Ferguson and Brockman 1980, Pilorge et al 1983, Tinkle and Dunham 1983). Interpretation of these differences within a conceptual framework such as r-K selection has however proven to be difficult, inconclusive or even unjustified.

Various authors have recently pointed out the inadequancies of the available data. Ballinger (1977, 1983) and Dunham (1982) have stressed the importance of considering temporal and non-evolutionary variations in life history characteristics and their causal sources within populations. These authors also emphasized that studies of the genetic basis of the variation in life-history traits are critically needed. In addition, long-term studies should establish to what extent differences in life-history traits among populations or species are coincident with predicted differences in population fluctuation (Ricklefs 1980). Grant (1983) advocated the integrated study of responses to environmental conditions at both the individual and population level. In the abscence of such data, tests of theories of life-history evolution will probably remain equivocal.

Herein we report results of a four-year study of a population of the lizard *Lacerta vivipara*, which was carried out with some of the above points in mind. We will deal here with the reproductive characteristics of that population and present data on the between-year and between-individual variation in some reproductive traits. In particular, we ask what factors contribute to

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the observed variation Our aim is not to discuss our results within a theoretical evolutionary framework but rather to contribute to the data base which may allow future tests of theories of life-history evolution in lizards

2 Material and methods

2.1. Animals, study area and general procedures

Lacerta vivipara is a small (adult body length (snout-vent, SVL, 45–65 mm). diurnal, insectivorous lizard which is found over a wide range in Europe and central Asia. It is a ground-dwelling species that behaves like a typical heliotherm This live-bearing lizard reproduces once a year and has a distinct annual reproductive cycle Mating and ovulation occur in April and May respectively, the young are born during the last week of July and the first half of August (Bauwens and Verheyen 1985) The lizards hibernate from October to the end of February (adult males) or the onset of April (adult females and immature lizards) (Bauwens 1981).

Data were gathered during the course of a population study conducted (by D B) during August 1977–May 1981 Some additional data were gathered in July 1981. Lizards were studied in a 62×41 m fenced plot located in the Belgian national nature reserve "de Kalmthoutse heide" (Kalmthout (51°25′N–4°25′E), province of Antwerp, Belgium) The vegetation of the study area is characteristic of moist heathland (see Bauwens and Thoen 1981 for a detailed description).

Lizards were captured by hand, marked individually by toe-clipping and released after noting identity, sex, reproductive condition, snout-to-vent length (SVL, to nearest 0.1 mm), tail length, and weight (to nearest 0 01 g on a portable electric Mettler P1210 balance)

Three age classes could be distinguished by body length: juveniles (born during the current activity season), subadults (born during the preceding year) and adults (in at least their third season). Within the adults we distinguished between lizards in third calendar year and lizards in at least their fourth season This distinction was possible because we marked and aged (either as juvenile, subadult or adult) all adult females during preceding years

2.2 Reproductive characteristics

Sexual maturity was assessed by noting the presence of oviducal eggs (pregnant females show a marked distension of the body) or the presence of a mating scar (all mated females that were subsequently recaptured proved to be gravid) The number of oviducal eggs could be counted by carefully palpating the females' abdomens

During 1979 and 1980 pregnant females were placed individually in open air vivaria just prior to parturition (as estimated by the amount of distension of the body). In these females, the number of young could be counted directly after birth This number always equalled the number estimated by palpation. Clutch weight was calculated in these females as the difference between female weights just before and after parturition. The average egg mass for each litter was estimated as the total clutch weight divided by the number of young in that clutch; an estimate of the variation of egg mass within clutches could not be obtained. Following their birth, juveniles were marked, weighed and together with their mother released within her home range.

Size adjusted body weight (SABW) was used as an index for the general body condition of a female. SABW of an individual female was estimated by its deviation (observed value minus predicted weight) from the relation, calculated for all females, between body weight and SVL (both variables log-transformed) We assume that a female's physical constitution (SVL and SABW) just before or at ovulation, rather than at some later time, will influence her reproductive performance. Therefore, measurements of SVL and body weight during May (approx. timing of ovulation) were used to obtain estimates of SVL and SABW

2 3. Environmental variation

Records of daily maximum temperatures were available from the weather station at Essen (4 km NNE), duration of sunshine was recorded at the station of Ukkel (34 km SSW) (source: Maandberichten van het K.M.I : Klimatologische waarnemingen) These records provide relative data on the annual and seasonal variation in weather conditions at the study site.

Ground-dwelling spiders (mainly *Lycosa* spp) were captured in pitfall traps (45×15×15 cm), located at both sides of the fence surrounding the study plot and used to trap dispersing lizards (see Bauwens and Thoen 1981 for a detailed description) Traps were installed and removed daily at known times, and the number of spiders trapped was counted at the end of each day, allowing expression of the data as number of spiders captured per trap-hour. These estimates provide indices of the relative abundance of only a fraction of the available prey However, Araneida are important prey for *L. vivipara,* representing 20–30% of the total number of prey (Avery 1962, 1966, Itamiës and Koskela 1971, Koponen and Hiëtakangas 1972, Pilorge 1982b) and 40–45% of the total prey volume (Itamiës and Koskela 1971, Koponen and Hiëtakangas 1972)

3. Results

3.1. Environmental variation

Data on weather conditions during each year of study are summarized in Tab 1. Weather conditions, particularly amounts of solar radiation and air temperatures, affect activity times (Avery 1971, 1976, House et al 1980) and rates of food intake (Avery 1971, 1984) in this temperate zone lizard and can hence be considered as

Tab. 1. Summary of meteorological data during different periods and years (see text for definition of 'assimilation period'). T_m: average daily maximum temperature (°C); H_s: total duration of sunshine (h.min).

	1978		1979		1980		1981	
	T_m	H_s	T_m	H_s	T_m	H_s	T_m	H_s
Apr.–May	15.2	309.55	15.0	308.30	15.7	393.30	15.9	300.35
Jun.–Jul.	20.5	316.45	21.0	291.00	20.2	272.20	20.2	257.50
Aug.–Sep.	20.0	265.05	20.4	336.00	21.6	322.45	21.3	322.00
Apr.–Sep.	18.6	891.55	18.8	935.30	19.2	988.35	19.1	880.25
Assimilation period	17.5	594.35	17.5	573.35	18.1	729.30	18.8	623.20

potentially important proximal factors affecting reproductive performances. Lizards assimilate the quantity of lipids necessary for producing the clutch during the interval between parturition and hibernation (August-September) of the preceding activity season and during the period between emergence from hibernation and ovulation (April-May) (Hahn and Tinkle 1965, Avery 1975, Derickson 1976a, 1976b). This interval has been termed the "assimilation period" (Tab. 1); weather conditions during this period, rather than at other times, are considered to be the most likely factors to affect reproduction.

Estimates of spider abundance (Fig. 1) suggest that more prey was available in 1979 than in 1980. The mean estimate for each month in 1979 was significantly greater than that for the corresponding month in 1980 (Mann-Witney U-tests, $P \leq 0.05$).

3.1. Sexual maturity

Data on body length during May of reproductive and immature females are shown in Fig. 2. None of the females with a body size (SVL) ≤ 42 mm were reproductive. The smallest reproductive female had a size of 43 mm, whereas the largest immature lizard measured 45 mm. All females ≥ 46 mm were reproductive. Hence a SVL of 43–45 mm can be considered as the minimum size of reproductive females. Lizards surpass this size in their third (age: 21 months) or fourth (age: 33 months) season.

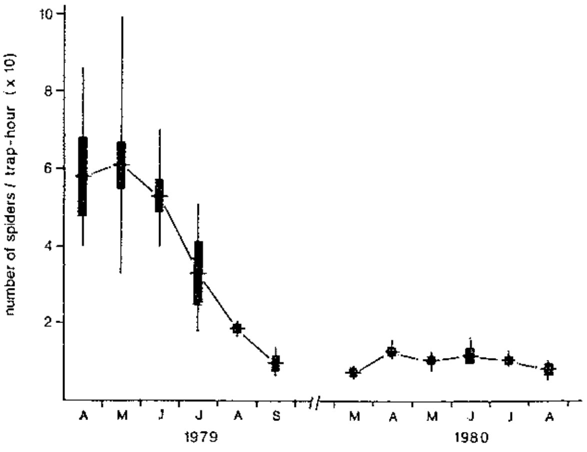

Fig. 1. Monthly estimates of the relative abundance of spiders in 1979 and 1980. Shown are the mean (horizontal line) ± 1 SE (vertical bar) and the range (vertical line).

The percentage of females maturing in their third season varied considerably between years ($G = 29.993$, 3 df, $P < 0.001$; Tab. 2) and was correlated with the average SVL of this cohort ($r = 0.960$, $P < 0.05$). Thus, the relative number of reproducing third calendar year females is largely dependent on the body size distribution of this group at the time of ovulation (May). All ≥ 4th year females were sexually mature.

3.2 Clutch size

Mean clutch size of reproductive females varied among years (ANOVA: $F = 3.721$, 3 and 96 df, $P < 0.02$; Tab. 2). Litter size was related to SVL in each year of study (Fig. 3; $P < 0.001$ in all cases) and there were significant differences in female size between years (ANOVA: $F = 6.510$, 3 and 96 df, $P < 0.001$; Tab. 2). An analysis of covariance was used to test for differences between the yearly clutch size-SVL relations. This analysis revealed no significant differences between slopes ($F = 1.570$, 3 and 92 df, $P > 0.20$) and intercepts ($F = 1.099$, 3 and 95 df, $P > 0.30$) of the regression equations. Accordingly, the adjusted means of clutch size in all years were comparable (Tab. 2). Observed variation among years in mean litter size was therefore explained by differences in body lengths of the reproductive females.

Next, we analysed among-individual differences in clutch size. We used a stepwise multiple regression analysis to determine the relations between litter size and the independent variables SVL, SABW and mean egg mass. These data were available for a subsample of 25 females reproducing in 1979 or 1980.

Clutch size was significantly related to SVL ($r = 0.747$, $P < 0.001$). Mean egg mass and SABW did not account for a significant fraction of the remaining variance in litter size. So, of the variables considered here, the number of young produced was only related to SVL.

In a further step, we concentrated on analysing the residual variance in litter size, by using deviations from the yearly clutch size-SVL relations as estimates of SVL-adjusted litter size (SALS). In 17 individual fe-

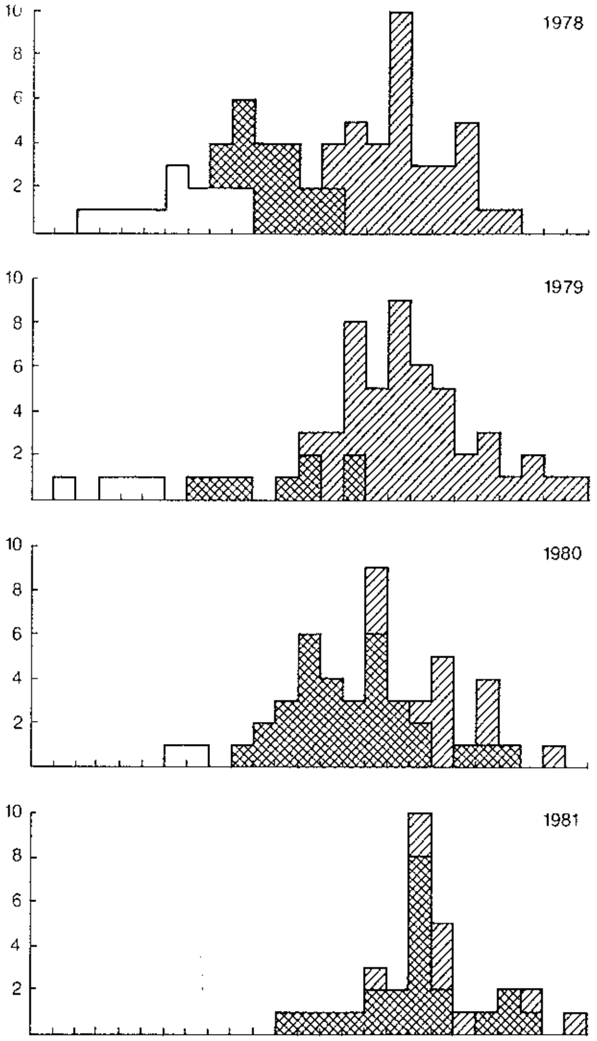

Fig. 2. Body size distributions of adult females as measured during May in different years. We distinguished between non-reproductive 3rd calendar year females (open), reproductive 3rd year females (cross-hatched) and reproductive ≥ 4th year females (hatched).

males, we determined clutch sizes during successive years (one female in 4 years, one in 3 years, fifteen in 2 years). These data allow partitioning of the phenotypic variance in SALS into variance within individuals and variance among females. A significant fraction of the variation in SALS was due to differences between females (ANOVA: $F = 3.532$, 16 and 20 df, $P < 0.01$), yielding a repeatability-estimate (± 1 SE) equalling 0.538 ± 0.167. Hence, approximately half of the variance in SALS is due to variation among females.

3.3. Clutch weight

Mean clutch weight at parturition equalled 1.68 g ($s = 0.44$, $n = 31$). Variation in clutch weight was analysed as a function of litter size, female size (SVL) and SABW. Clutch weight increased both with litter size ($r = 0.876$, $P < 0.001$) and SVL ($r = 0.731$, $P < 0.001$). The former variable was selected as the most significant factor in a stepwise regression analysis. Subsequently calculated partial correlations were not significant ($P > 0.20$), indicating that SVL and SABW did not account for a significant fraction of the remaining variance in litter weight. The increase in clutch weight with female size must hence be attributed to increasing egg numbers.

3.4 Egg weight

Mean egg mass (at parturition) for all litters was 0.379 g ($s = 0.042$, $n = 31$). Average egg mass was somewhat higher in 1979 than in 1980 (Tab. 3), but the difference was not significant ($t = 1.422$, 29 df, $P > 0.10$). Mean egg mass in a litter was not correlated with clutch size, SALS, SVL or SABW.

3.5. Hatchling weight

Data on juvenile weight at birth are summarized in Tab. 3. Juveniles were heavier in 1979 than in 1980 ($t = 3.314$, 102 df, $P < 0.01$). Average hatchling weight in each litter comprised about half of the mean egg mass (1979: $\bar{x} = 49\%$, $s = 9$, $n = 10$; 1980: $\bar{x} = 47\%$, $s = 7$, $n = 17$). In both years a significant fraction of the vari-

Tab. 2. A. Proportion of reproducing females and SVL (mean ±1 SE) as measured during May, in the two adult age groups in different years. B. Clutch size (mean ±1 SE), SVL as measured during May, and adjusted mean clutch size in different years.

	1978	1979	1980	1981
A 3 year ♀♀				
% repr.	52.8	66.7	94.3	100.0
SVL	45.0±0.5	44.8±1.2	50.0±0.5	53.2±0.6
n	36	12	35	22
≥4 year ♀♀				
% repr	100.0	100.0	100.0	100.0
SVL	52.8±0.3	53.4±0.4	54.6±0.7	54.8±0.9
n	38	46	13	9
B Clutch size	3.9±0.2	4.5±0.2	4.4±0.2	4.8±0.2
SVL	51.±0.6	54.1±0.7	52.4±0.6	54.8±0.7
Adjusted clutch size	4.3±0.1	4.2±0.1	4.5±0.1	4.4±0.1
n	27	22	27	24

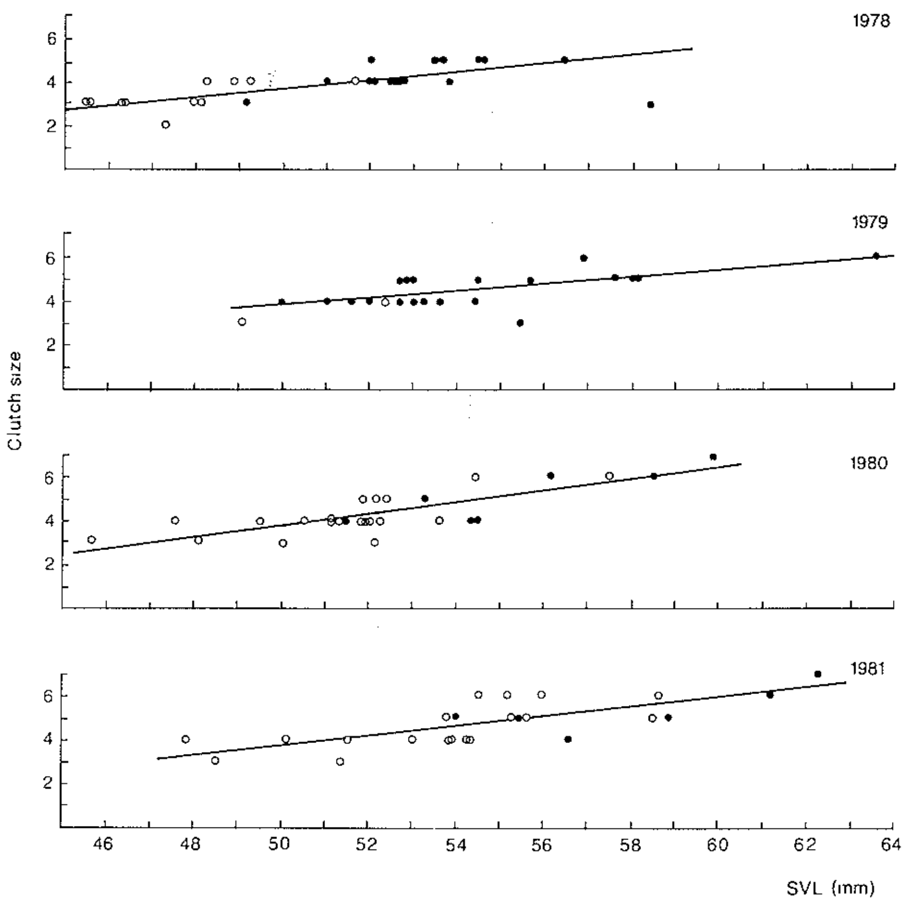

Fig. 3. Relations between clutch size and female length (SVL) in different years. Open symbols: 3rd calendar year females; solid symbols: ≥ 4th year females

ance in juvenile weight was due to differences among litters (ANOVA: $P < 0.001$ in both analyses). We found no significant correlations between mean hatchling weight in each litter and the independent variables clutch size, SALS, SVL, SABW and mean egg mass. Consequently, the low SALS and high mean egg mass in the 1979 females whose young were weighed (Tab. 3), do not explain the high weight of the 1979 juveniles.

Tab. 3. Size-adjusted litter size (SALS), mean egg mass for each litter and mean individual hatchling weight in 1979 and 1980. Shown are the mean ± 1 SE and sample size (in brackets) (SALS is shown only for those females whose clutches and young were weighed)

	SALS	Mean egg mass (g)	Hatchling weight (g)
1979	−0.243±0.148 (13)	0.392±0.013 (13)	0.190±0.005 (33)
1980	0.135±0.132 (18)	0.370±0.009 (18)	0.172±0.003 (71)

4. Discussion

Two major sources of variation may contribute to the phenotypical variance in life-history traits within a population: (1) variation between females within each year, and (2) variation between years.

Much of the observed among-individual variance in reproductive traits was attributable, either directly or indirectly, to female size. In our population, females mature in their third activity season, provided that they attain a body size of approximately 43–45 mm during May; otherwise they delay reproduction to their fourth activity season. These data suggest that sexual maturity is associated with attaining a minimum body size, rather than a minimum age. This suggestion is confirmed by the results obtained by Heulin (1985) in a French population of *L. vivipara,* where a proportion of the females surpass a size of 40–42 mm and are sexually mature in their second activity season (our subadults).

Clutch size, and consequently clutch weight, increased with female length during each year of study, confirming results of previous studies on this lizard (Avery 1975, Pilorge et al. 1983, Heulin 1985).

Consistency of size adjusted litter size across years was estimated in females for which pregnancies were observed in successive years. The significant repeatability score indicated that individual females are likely to produce litters of a similar length-adjusted size in different years. Such consistent differences may result either from genetic or from lasting differences in environmental conditions among individuals (Falconer 1981). The notion of repeatability bears a relation to population genetics in that it sets an upper limit to the possible heritability score (the ratio of additive genetic variance to phenotypic variance) of a trait (Falconer 1981). Although we cannot distinguish between the contribution of genetic and environmental factors to the differences among females, our results do not exclude the possibility that clutch size is heritable in our population.

Hatchling mass varied significantly among clutches, suggesting that some phenotypical attribute of the female contributes to the variation in juvenile size. The proximal causes of this variability however remain obscure, as no relations with other considered traits were detected. The absence of a relation between mean hatchling weight and mean egg mass in a litter is remarkable, and should probably be attributed to differences among clutches in the relative mass of membranes and extra-embryonic water. This parallels the finding by Pilorge et al. (1983) of considerable differences between years and between populations in the ratio total offspring weight/clutch weight.

Although absolute reproductive output varied markedly among years, size-adjusted reproductive performance remained approximately constant during the course of this study. Among year variation in the relative number of reproducing females and in clutch size was therefore attributable to differences in the body size distributions of the adult females. In contrast, studies of other lizards have revealed significant between-year variation in various reproductive traits (clutch frequency, clutch size and weight) (Hoddenbach and Turner 1968, Vinegar 1975, Martin 1977, Ballinger 1977, Vitt et al. 1978, Dunham 1981, Turner et al. 1982 but see Van Loben Sels and Vitt 1984). Most relevant in this respect are the studies of Ballinger (1977) and Dunham (1981), showing the effect of food availability on reproduction in lizard populations. Significant among-year variation in reproductive traits was also evident in a population of *L. vivipara* studied by Pilorge et al. (1983). Appropriate analysis of their data revealed significant variation in clutch size in one of their populations (Lac Pavin, France) (SVL-adjusted means: 1978: 6.4; 1980: 5.2; 1981: 5.4). Between-year differences in size-adjusted clutch weight were also apparent in that population (Pilorge et al. 1983). Panigel (1956), whose lizards were collected within the same area, reported considerable between-year variation in the timing of ovulation and parturition. During the course of our study no such variability in the timing of reproduction was apparent (Bauwens and Verheyen, 1985).

The relative constancy of reproductive investments in our population suggests that fluctuations of environmental conditions remained within levels that enabled females to assimilate the energy required for the accomplishment of a typical reproductive performance. In *L. vivipara,* rates of food consumption are probably dependent on the amount of food available, and are known to be directly proportional to the period for which activity temperatures can be maintained through behavioural thermoregulation (Avery 1971, 1984). Abilities to thermoregulate and activity times of this lizard are strongly dependent on air temperatures and the duration of sunshine (Avery 1971, 1976, House et al. 1980, Van Damme et al. in press). Avery (1984) has experimentally demonstrated that growth rate in juvenile *L. vivipara* is proportional to the rate of food intake. Weather conditions (and food availability) are therefore expected to induce changes in growth rates through affecting activity times (Avery 1971, House et al. 1980) and rates of food intake (Avery 1971, 1984). This implication is confirmed by the finding that seasonal and annual variation in growth rate and body weight of juvenile and subadult lizards was related to variations in weather conditions and food availability in our study population (Bauwens 1985). Hence, observed fluctuations in weather conditions and food availability were seemingly severe enough to affect growth rates of juvenile and subadult lizards, and consequently induced delayed among-year differences in the body size distributions and absolute reproductive output of the adult females. In contrast, size-specific reproductive performances were constant and apparently not affected by observed variations in environmental factors.

Several hypothesis might explain this coincidence of similar reproductive investments with variable growth rates across years. First, it may be argued that rates of energy intake are not affected by the same environmental conditions in adult females and non-reproductive lizards. This hypothesis is however not supported by the findings of Avery (1971), who convincingly demonstrated that rates of food intake are dependent on weather conditions in lizards of all age classes.

Second, it can be suggested that females allocate but a minor fraction of their energy into reproduction. The production of the clutch in *L. vivipara* has been estimated to represent 7–9% (Avery 1975) or 3–10% (Pilorge 1982a) of the annual assimilation, and 28–35% of the energy assimilation during the period between emergence from hibernation and ovulation (Avery 1975). Especially the latter estimate indicates that reproductive investment is not a negligible portion of this lizard's energy budget.

Alternatively, it may be hypothesized that females would respond to periods of decreased resource availability by allocating a higher proportion of the available energy toward reproduction. Although this hypothesis remains untestable in the absence of data on energy budgets in individual females, other studies have supported the idea of flexible energy allocation in lizards

We have previously (Bauwens and Verheyen 1985) suggested that differences in the timing of reproduction between individual female *L. vivipara* are induced by a size-related shift in the allocation of energy toward growth or reproduction Van Devender (1978) provided convincing evidence that in response to decreased food levels, females of the lizard *Basiliscus basiliscus* facultatively modify growth rates in favour of reproductive activities

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References

Avery, R. A 1962. Notes on the ecology of *Lacerta vivipara* – Brit J. Herpet 2: 36–38.

– 1966 Food and feeding habits of the common lizard (*Lacerta vivipara*) in the west of England – J Zool. (London) 149: 115–121

– 1971. Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin – J Anim Ecol 40: 351–365.

– 1975 Clutch size and reproductive effort in the lizard *Lacerta vivipara* – Oecologia (Berl.) 19: 165–170.

– 1976. Thermoregulation metabolism and social behaviour in Lacertidae – In: d'A Bellairs, A and Cox, C. B (eds), Morphology and biology of reptiles Linn Soc Symp. Ser nr 3. London, pp. 245–259

– 1984 Physiological aspects of lizard growth: the role of thermoregulation. – Symp Zool Soc. Lond. 52: 407–424

Ballinger R E 1973 Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *S poinsetti*) – Ecology. 54: 269–283.

– 1977 Reproductive strategies: food availability as a source of proximal variation in a lizard – Ecology 58: 628–635

– 1979 Intraspecific variation in demography and life history of the lizard *Sceloporus jarrovi* along an altitudinal gradient in southeastern Arizona – Ecology 60: 901–909

– 1983 Life-history variations – In: Huey, R B , Pianka, E R and Schoener T. W (eds). Lizard ecology Studies on a model organism Harvard University Press. Cambridge. pp. 241–260.

Bauwens D. 1981 Survivorship during hibernation in the European common lizard *Lacerta vivipara* – Copeia 1981: 741–744.

– 1985 Demografische kenmerken en aantalsdynamiek in een populatie van de Levendbarende Hagedis (*Lacerta vivipara*). – Ph. D. thesis, University of Antwerp.

– and Thoen, C. 1981 An enclosure design allowing quantification of dispersal in lizard population studies – Brit J Herpetol 6: 165–168.

– and Verheyen R F 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females – J Herpetol 19: 353–364.

Damme, R Van. Bauwens, D and Verheyen, R F 1987. Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara* – Herpetologica (In press).

Derickson W. K. 1976a Ecological and physiological aspects of reproductive strategies in two lizards – Ecology 57: 445–458.

– 1976b. Lipid storage and utilization in reptiles – Am. Zool 16: 711–723

Devender, R. W Van 1978 Growth ecology of a tropical lizard, *Basiliscus basiliscus* – Ecology 59: 1031–1038.

Dunham, A E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. – Ecology 59: 770–778.

– 1981. Populations in a fluctuating environment: the comparative population ecology of the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus* – Misc. Publ Univ. Mich Mus. Zool. 158: 1–62.

– 1982 Demographic and life-history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life-history phenomena in lizards. – Herpetologica 38: 208–221

Falconer, D. S 1981. Introduction to quantitative genetics (2nd ed.) – Longman. New York.

Ferguson, G W. and Brockmann, T 1980 Geographic differences of growth rate of *Sceloporus* lizards (Sauria: Iguanidae). – Copeia 1980: 259–264

Grant, P 1983 Conclusion: Lizard ecology, viewed at a short distance. – In: Huey, R B., Pianka. E R. and Schoener. T. W. (eds). Lizard ecology. Studies of a model organism Harvard University Press, Cambridge. pp 411–417.

Hahn, W E. and Tinkle, D. W. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana* – J Exp Zool. 158: 79–86

Heulin, B 1985. Maturité sexuelle et age à la première reproduction dans une population de plaine de *Lacerta vivipara*. – Can. J. Zool 63: 1773–1777.

Hoddenbach, G. A. and Turner, F. B. 1968. Clutch size of the lizard *Uta stansburiana* in southern Nevada – Am Midl Nat. 80: 262–265

House, S. M., Taylor, P. J. and Spellerberg, I F 1980 Patterns of daily behaviour in two lizard species: *Lacerta agilis* L and *Lacerta vivipara* Jacquin – Oecologia (Berl) 44: 396–402

Itamiës, J and Koskela, P. 1971 Diet of the common lizard (*Lacerta vivipara* Jacquin) – Aquilo (Ser Zool.) 11: 37–43.

Koponen, S and Hiëtakangas H 1972 Food of the common lizard (*Lacerta vivipara*) on a peat bog in southwestern Finland – Ann. Zool. Fenn 9: 191–192.

Martin R F 1977 Variation in reproductive productivity of range margin tree lizards *Urosaurus ornatus* – Copeia 1977: 83–92.

Panigel, M 1956 Contribution a l'étude de l ovoviviparité chez les reptiles: gestation et parturition chez le lézard vivipare *Zootica vivipara* – Ann Sci Nat (Zool) 18: 569–668

Pianka, E R 1970 Comparative ecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. – Ecology 51: 703–720

Pilorge T 1982a Ration alimentaire et bilan énergétique individuel dans une population de montagne de *Lacerta vivipara* – Can J Zool 60: 1945–1950

– 1982b, Régime alimentaire de *Lacerta vivipara* et *Rana temporaria* dans deux populations sympatriques du Puy-de-Dome. – Amphibia-Reptilia, 3: 27–31

– Xavier, F. and Barbault. R 1983. Variations in litter size and reproductive effort within and between some populations of *Lacerta vivipara*. – Holarct. Ecol. 6: 381–386

Ricklefs, R. E. 1980 Ecology (2nd ed.). – Nelson

Schoener. T. W. and Schoener, A 1978. Estimating and interpreting body-size growth in some *Anolis* lizards – Copeia 1978: 390–404.

Tinkle, D W. 1969 The concept of reproductive effort and its relation to the evolution of life histories of lizards – Am. Nat 103: 501–516.

– and Ballinger, R. E. 1972. *Sceloporus undulatus*: A study on the intraspecific comparative demography of a lizard – Ecology 53: 570–584.

– and Dunham, A E 1983 Demography of the tree lizard.

Urosaurus ornatus. in central Arizona. – Copeia 1983: 585–597.

– . Wilbur, H. H. and Tilley, S. G. 1970. Evolutionary strategies in lizard reproduction. – Evolution 24: 55–74.

Turner, F. B., Medica, P. A., Bridges, K. W. and Jennrich, R. I. 1982. A population model of the lizard *Uta stansburiana* in southern Nevada. – Ecol. Monogr. 52: 243–259.

Van Loben Sels, R. C. and Vitt, L. J. 1984. Desert lizard reproduction: seasonal and annual variation in *Urosaurus ornatus* (Iguanidae). – Can. J. Zoöl. 62: 1779–1788.

Vinegar, M. B. 1975. Life history phenomena in two populations of the lizard *Sceloporus undulatus* in southwestern New Mexico. – Am. Midl. Nat. 93: 388–402.

Vitt, L. J. and Congdon, J. D. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. – Am. Nat. 112: 595–608.

– . Van Loben Sels, R. C. and Ohmart, R. D. 1978. Lizard reproduction: annual variation and environmental correlates in the iguanid lizard *Urosaurus graciosus*. – Herpetologica 34: 241–252.