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Comparative demography of sympatric populations of *Lacerta vivipara* and *Lacerta agilis*

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Summary. A mark-recapture study was carried out in sympatric populations of *Lacerta agilis* and *Lacerta vivipara* in the Netherlands from 1976 to 1982. In most years the age structure of both populations was pyramidal. For both species life expectation of females was higher and on average they did live longer. Hence the sex ratio for adults deviated significantly from 1.0 in favour of females. Maximum age for *Lacerta vivipara* was 8 years (female) and for *Lacerta agilis* 12 years (male). The density of both species fluctuated around 100/ha. The biomass of *Lacerta agilis* was twice that of *Lacerta vivipara.* In *Lacerta vivipara* the 3rd and 4th calendar year class supplied 78% of total net reproduction; in *Lacerta agilis* the 4th, 5th, and 6th calendar year classes supplied 68%. In both populations the population replacement rate was 2. Population turnover time was 4.83 years for *Lacerta agilis* and 2.81 for *Lacerta vivipara.* The life history strategy of the *Lacerta vivipara* population is compared with six other European *Lacerta vivipara* populations.

Key words: Demography – *Lacerta agilis* – *Lacerta vivipara* – Life history strategy – Life table

Population studies of lizards give an impression of variation in life history strategies within species (e.g. Tinkle and Ballinger 1972; Ballinger 1979; Dunham 1982) or among various species (e.g. Tinkle 1972; Ballinger 1973). The variations in demographic characteristics are presumed to be adaptive responses to external conditions (Tinkle 1969). One of the best studied species in Europe is the viviparous lizard (*Lacerta vivipara*). The demography of this species has been studied in mountain populations in central France (Pilorge 1981, 1982; Pilorge and Xavier 1981) and in Austria (Broers and Clerx 1981; Clerx and Broers 1982), as well as in a number of lowland populations in England (Avery 1975a), in Brittany (Heulin 1984, 1985a), in Belgium (Bauwens and Verheyen 1980; Bauwens 1985) and in the Netherlands (Lenders 1985). In all these cases, however, these were unmixed *Lacerta vivipara* populations considered singly. Therefore this study is the first one of the population dynamics in sympatric *Lacerta vivipara* and *Lacerta agilis* populations.

Material and methods

The study was conducted from 1976 to 1982 on a 1.2-ha test site (80 by 150 m) on the reserve "de Hamert" at Bergen in the Netherlands. The test site was on a river dune top, so that it was divided into a north-facing and a south-facing slope (0.53 ha and 0.67 ha respectively). On the north-facing slope vegetation was mainly *Calluna vulgaris*, *Molinea caerulea*, and *Deschampsia flexuosa.* The south-facing slope was dominated by homogenous *Calluna vulgaris* vegetation. To the west the test site was bordered by a pine forest and in the transition zone to this forest grew some *Betula verrucosa* and *Pinus sylvestris* trees. On the test site four different reptile species were found: the viviparous lizard *Lacerta vivipara* Jacquin, the sand lizard *Lacerta agilis agilis* L., the slow worm *Anguis fragilis fragilis* L., and the smooth snake *Coronella austriaca austriaca* Laurenti.

The animals were captured by hand and individually marked by toe-clipping. In every year of the study each capture was recorded as follows: species, marking number, time, capture spot, sex, age, snout-vent length, tail length (primary and secondary if present), weight, and details such as presence of parasites, sloughing stage, scars, and reproductive stage. The total number of captures was 1900 for *Lacerta vivipara* and 3777 for *Lacerta agilis*, including those just outside the test site.

The test site was visited almost daily during each active season (mid-March–mid-October). Every year this high searching intensity supplied an accurate picture of the animals living in the test site (except the juveniles) and it enabled us to determine the minimum population sizes at the beginning of each season.

The numbers of the various age classes per season were corrected afterwards if an animal was captured in later years only. Marking the animals captured just outside the test site enabled us to correct for migrators and animals living on the border-line. Some 3% of the animals captured offered some problems when determining their exact age. In that case a minimum age was estimated by comparing weight, length, and reproductive stage (for females) with groups of animals whose age was known in that year. This method of minimum population estimation does not apply for the determination of the minimum number of juveniles, because they are only present during a short period of the season and are liable to a high mortality rate. The minimum number of juveniles was estimated using three types of data:

1. The minimum number of females present within the test site, per year and per age-class

2. The mean clutch size per pregnant female, of each year-class

3. The fractional participation of females in reproduction, per year and per age-class, deduced from all captures

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The mean clutch size of *Lacerta vivipara* females was established by counting the number of egg bulges on the sides of pregnant females. After comparison with X-ray photographs these counts appeared to be reliable. As a result of its relatively short visible pregnancy too few such countings were done for *Lacerta agilis*. Therefore the clutch sizes of various age classes of this species were estimated using the relation (as given in the literature) between body-size (indirectly the age) and clutch size (Scepotev 1948; Tertyshnikov 1978). In 1976, 1978, and 1985 we tested these estimates by letting a total of 27 females from our test site deposit their eggs in a vivarium. The data confirmed the relation between clutch size and age and/or body size.

In the months in which the females showed signs indicating successful participation in reproduction (visible pregnancy and/or deep skin folds on the sides) we calculated the fraction of females showing these signs, divided by year and age-class. Due to the small numbers of 5th calendar year females of *Lacerta agilis* we were not able to determine a reliable fraction for this age class in each separate year. Therefore we took the average of all data of all years for this age-class. Owing to the low number of captures in the relatively short period of visible pregnancy, we also obtained little data for the 6th calendar year and older females. Among the animals captured in that period, participation appeared to be 100% in all cases.

Results

1 Age structure and sex ratio

In most years both populations showed a pyramidal age structure (Tables 1 and 2). In 1977 the numbers of 2nd c.y. (calendar year) animals, however, were very small compared to the other year classes. The consequences of this are seen again in later years, though somewhat weakened. The causes for the small number of 2nd c.y. animals of both species in 1977 were overestimates of the numbers of juveniles born in 1976 and/or high mortality in 1st c.y. animals in 1976. This is probably related to the long, dry, and hot summer of 1976 (see Discussion). Particularly in 1977, the number of 1st c.y. *Lacerta vivipara* is rather low. The possible causes of this phenomenon will be discussed later.

Sex can be determined in both species for animals with a minimum snout-vent length of about 40 mm, which is reached in the course of the second active season. For the 2nd c.y. animals we found no significant deviation from

Table 1. Minimum population size and sex ratio (SR) over the period 1976–1982 for *Lacerta vivipara* (c.y. = calendar year, SU = sex unknown, T = total, ″ = significantly different from 1.0)

		1976	1977	1978	1979	1980	1981	1982	1976–1982
Juveniles	SU	114	65	90	131	149	152	112	813
Subadults	♂♂	30	12	14	22	44	24	33	179
(2nd c.y.)	♀♀	22	9	13	22	31	22	20	139
	SU	14	3	14	13	12	13	9	68
	T	66	24	41	57	87	49	62	386
	SR	1.36	1.33	1.08	1.00	1.42	1.09	1.65	1.29″
Adults	♂♂	22	27	18	15	19	31	33	165
	♀♀	52	29	26	25	28	33	27	220
	T	74	56	44	40	47	64	60	385
	SR	0.42″	0.93	0.69	0.60	0.68	0.94	1.27	0.75″

Table 2. Minimum population size and sex ratio (SR) over the period 1976–1982 for *Lacerta agilis* (c.y. = calendar year, SU = sex unknown, T = total, ″ = significantly different from 1.0)

		1976	1977	1978	1979	1980	1981	1982	1976–1982
Juveniles	SU	145	130	130	121	94	104	121	845
Subadults	♂♂	22	6	14	18	24	25	18	127
(2nd c.y.)	♀♀	36	9	11	22	25	23	17	142
	SU	8	4	10	12	4	9	7	54
	T	66	19	35	52	53	57	42	324
	SR	0.61	0.67	1.27	0.82	0.96	1.09	1.06	0.89
Subadults	♂♂	14	21	3	12	12	11	16	89
(3rd c.y.)	♀♀	4	31	7	8	17	20	13	100
	T	18	52	10	20	29	31	29	189
	SR	3.50″	0.68	0.43	1.50	0.71	0.55	1.23	0.89
Adults	♂♂	22	18	22	12	18	19	20	131
	♀♀	31	24	33	23	18	21	26	176
	T	53	42	55	35	36	40	46	307
	SR	0.71	0.75	0.67	0.52	1.00	0.90	0.77	0.74″

Table 3. Density (*N*/ha) and biomass (g/ha) estimations for *Lacerta vivipara* and *Lacerta agilis*

	1976	1977	1978	1979	1980	1981	1982	$x \pm SD$
Density								
L. vivipara	118	69	71	84	116	94	103	93.6 ± 20.0
L. agilis	114	94	83	90	99	108	97	97.9 ± 10.5
Total	232	163	154	174	215	202	200	191.4 ± 28.6
Biomass								
L. vivipara	–	182	207	235	336	379	336	279.2 ± 81.3
L. agilis	–	524	494	507	568	694	567	559.0 ± 72.8
Total	–	706	701	742	904	1073	903	838.2 ± 147.8

a sex ratio of 1.0 in all the years. When all years were added together, the sex ratio of subadult *Lacerta vivipara* appeared to be significantly more than 1.0 (males:females; binomial test). For adult *Lacerta vivipara* we found a sex ratio significantly different from 1.0 only in one year. The sex ratio of all adults of all years added together turned out to be significantly lower than 1.0 for the two species. In this age category the females live longer than the males (cf. also Tables 6 and 7).

2 Density and biomass

For both species the densities and biomasses were calculated for each separate year (Table 3). Biomass was calculated by multiplying the minimum numbers of females and males of a certain age by the mean weight of these groups in that year, excepting 1976 when no data on the weight of the animals were available. Both species turn out to occur in about the same densities. The share of *Lacerta agilis* in the total biomass, however, is twice that of *Lacerta vivipara*. Generally *Lacerta agilis* grows older, bigger, and heavier.

The juveniles were not included in the calculations. The densities of juveniles may over-influence the total picture; moreover, juveniles are not necessarily born in their mother's home range. The biomass of juveniles has partly been included in the calculations via the weight of pregnant females.

On the northern and southern slopes *Lacerta vivipara* reaches average densities over all the years together of 156 and 41/ha respectively, with corresponding biomasses of 401 and 160 g/ha respectively. For *Lacerta agilis* we calculated average densities on the northern and southern slope of 69 and 119/ha respectively, with biomasses of 367 and 714 g/ha respectively.

3 Reproduction

Starting from clutch size, the fractional participation in reproduction, and the minimum numbers of females within a certain year class, one can calculate per year class the absolute and the relative contribution to net reproduction (see Tables 4 and 5). Absolute mean net reproduction for *Lacerta vivipara* is 116 and for *Lacerta agilis* 121 juveniles per year. The 3rd and 4th c.y. females of *Lacerta vivipara* turn out to supply about 78% of net reproduction, whereas in *Lacerta agilis* net reproduction is mainly supplied by 4th, 5th, and 6th c.y. females (together 68%). The participation of 3rd c.y. *Lacerta vivipara* females in 1977 and of 4th c.y. *Lacerta agilis* females in 1978 turned out to be extremely low in comparison to other years, caused by the extremely dry summer of 1976.

The fecundity (mean egg production per female) in a certain age class appears to increase with age for both species (see *mx* in Tables 6 and 7). The average egg production of all pregnant females is 5.6 for *Lacerta vivipara* and 6.2 for *Lacerta agilis*. The contribution to net reproduction of a certain age class is expressed as $mxl'x$, in which $l'x$ is the number of females as a fraction of the starting number. Adding all $mxl'x$ values then produces the population replacement value = R0 (Tinkle 1972) which should be around 2.0 for stable populations. In the populations we studied this appeared to be the case.

4 Mortality and life table

Starting from the minimum population estimates, life tables (Tables 6 and 7) and survival curves (Fig. 1) can be drawn up for both species during the period 1976–1982. For both species it appears that on the average females have a higher life expectancy and do live longer. The maximum age found is 8 years for *Lacerta vivipara* (female) and 12 years for *Lacerta agilis* (male). In the life tables some critical phases can be distinguished. For *Lacerta agilis* these are the juvenile phase and the age at which the animals reproduce for the first time. For *Lacerta vivipara* we find this critical phase for the females but hardly for the males.

Juveniles were allocated half to the females and half to the males. The numbers of females and males in the 2nd c.y. animals were estimated on the basis of the ratio between females and males within the group which could be sexed. With the formula $T = \Sigma x' \cdot mxl'x/2$ (Tinkle 1972; x' = age in years) the population turnover time, i.e. the average life span of a generation, can be calculated (Table 8).

Discussion

When establishing the minimum numbers of juveniles we started from the numbers of females at the beginning of the season. Juveniles, however, are born later in the season and so the mortality of females in the intermediate months may well influence the real numbers of juveniles born. This problem might be avoided by establishing the minimum

Table 4. Mean clutch size (MCS) of pregnant females per age class (AC), relative participation in net reproduction (P) and absolute (A) and relative (R) contribution to net reproduction for the *Lacerta vivipara* population

AC	MCS		1976	1977	1978	1979	1980	1981	1982	1976–1982
2		P					0.053		0.063	0.020
	4.00	A					8		6	14
	(*N*=1)	R					5.4%		5.4%	1.7%
3		P	0.316	0.273	0.500	0.917	0.950	0.722	0.636	0.563
	5.23	A	60	27	24	58	84	79	37	369
	(*N*=31)	R	52.6%	41.5%	26.7%	44.3%	56.4%	52.0%	33.0%	45.4%
4		P	0.500	0.600	0.643	1.000	0.833	1.000	0.700	0.702
	5.88	A	41	32	45	18	44	47	37	264
	(*N*=16)	R	36.0%	49.2%	50.0%	13.7%	29.5%	30.9%	33.0%	32.5%
5		P		1.000	0.667	0.800	1.000	1.000	0.667	0.780
	6.25	A		6	21	35	6	19	25	112
	(*N*=8)	R		9.2%	23.3%	26.7%	4.0%	12.5%	22.3%	13.8%
6–8		P	1.000			1.000	1.000	1.000	1.000	1.000
	6.50	A	13			20	7	7	7	54
	(*N*=4)	R	11.4%			15.3%	4.7%	4.6%	6.3%	6.6%
Total		A	114	65	90	131	149	152	112	813

Table 5. Mean estimated clutch size (MCS) of pregnant females per age class (AC), relative participation in net reproduction (P) and absolute (A) and relative (R) contribution to net reproduction for the *Lacerta agilis* population

AC	MCS		1976	1977	1978	1979	1980	1981	1982	1976–1982
3		P							0.105	0.014
	4.0	A							5	5
		R							4.1%	0.6%
4		P	0.500	0.714	0.286	0.750	0.500	0.556	0.624	0.523
	4.5	A	27	26	23	20	14	30	39	179
		R	18.6%	20.0%	17.7%	16.5%	14.9%	28.8%	32.2%	21.2%
5		P	0.824	0.824	0.824	0.824	0.824	0.824	0.824	0.824
	6.0	A	40	35	15	54	15	5	30	194
		R	27.6%	26.9%	11.5%	44.6%	16.0%	4.8%	24.8%	23.0%
6		P	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	7.0	A	70	21	28	7	49	21	7	203
		R	48.3%	16.2%	21.5%	5.8%	52.1%	20.2%	5.8%	24.0%
7–10		P	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	8.0	A	8	48	64	40	16	48	40	264
		R	5.5%	36.9%	49.2%	33.1%	17.0%	46.2%	33.1%	31.2%
Total		A	145	130	130	121	94	104	121	845

Table 6. Life table for *Lacerta vivipara*, females and males (*x*=age in years)

x	*lx*		*dx*		*qx*		*ex*		*mx*	*mxl′x*
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♀
0	1000	1000	576	473	576	473	1.47	1.43	0.00	0.00
1	424	527	116	263	274	499	1.78	1.27	0.08	0.03
2	308	264	150	156	487	591	1.26	1.14	2.94	0.91
3	158	108	101	83	639	769	0.98	0.82	4.13	0.65
4	57	25	47	15	825	600	0.83	0.90	4.88	0.28
5	10	10	3	10	300	1000	1.40	0.50	6.50	0.07
6	7		5		714		0.79		6.50	0.05
7	2		2		1000		0.50		6.50	0.01
										R0=2.00

Table 7. Life table for *Lacerta agilis*, females and males (x = age in years)

x	lx		dx		qx		ex		mx	$mxl'x$
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♀
0	1000	1000	595	638	595	638	1.56	1.38	0.00	0.00
1	405	362	168	151	415	417	2.12	1.94	0.00	0.00
2	237	211	57	43	241	204	2.27	1.97	0.06	0.01
3	180	168	88	102	489	607	1.83	1.35	2.35	0.42
4	92	66	23	33	250	500	2.10	1.67	4.94	0.45
5	69	33	29	12	420	363	1.63	1.83	7.00	0.48
6	40	21	9	14	225	667	1.45	1.60	8.00	0.32
7	31	7	26	0	839	0	0.73	2.79	8.00	0.25
8	5	7	3	2	600	286	0.90	1.79	8.00	0.04
9	2	5	2	3	1000	600	0.50	1.30	8.00	0.02
10		2		0		0		1.50		
11		2		2		1000		0.50		
										R0 = 1.99

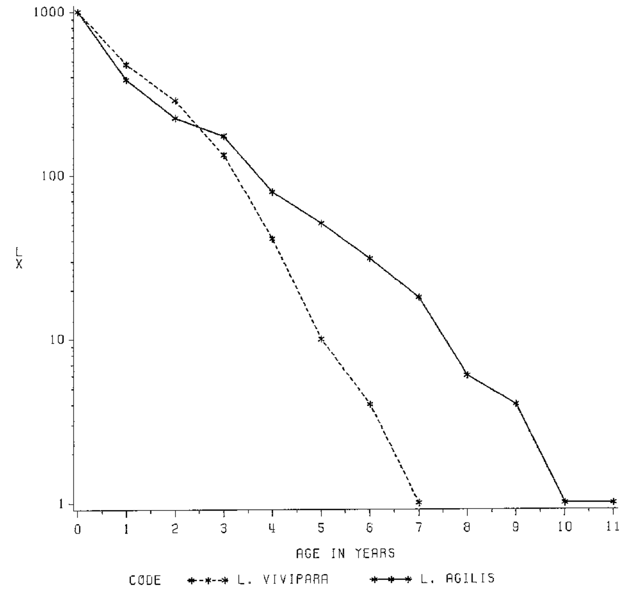

Fig. 1. Survivorship of *Lacerta vivipara* and *Lacerta agilis*

Table 8. Population turnover for both species in the Hamert population and for a pure *Lacerta vivipara* population elsewere in the Netherlands

Lacerta agilis	4.83
Lacerta vivipara	2.81
Lacerta vivipara	2.90 (Lenders 1985)

population size at the moment at which juveniles are born. This leads to the following disadvantages: an illogical division for other age classes; lower numbers of animals on which life tables can be based; and uncertainty as to the death date of the females (non-capture does not always mean death). The numbers of juveniles born, calculated by the above method, sometimes turned out to be even lower than the minimum number of subadults in the subsequent years.

For 2nd c.y. and older animals of *Lacerta vivipara* a sex ratio not significantly deviating from 1.0 is often given (Pilorge 1981; Avery 1975a). From the life tables it appears, however, that especially in the group of 3rd c.y. and older animals the females of this species often survive better (Lenders 1985; Pilorge and Xavier 1981; Heulin 1985a; and own data). In *Uta stansburiana* (Tinkle 1967), *Sceloporus undulatus* (Tinkle 1972), *Sceloporus graciosus* (Tinkle 1973), and *Sceloporus scalaris* (Ballinger and Congdon 1981) the adult females also turned out to survive better than the adult males. Bauwens (1985) found this only at the beginning of his study, but he points to a relation between his study activities and an increased mortality for the 4th c.y. and older females. In good habitats with high densities the sex ratios for *Anolis sagrei* (Schoener and Schoener 1980) and of *Lacerta agilis* (Olsson 1984) were found to be lower than 1.0 male:female, and the females of these species were considered territorial.

The very small numbers of subadults in 1977 in both species are probably the result of the extreme weather conditions (drought) in the summer of 1976. A similar phenomenon occurred in the drier habitats of the *Lacerta vivipara* population studied by Lenders (1985), while it could not be found in the moister habitats. So far it is not clear exactly when this mortality took place, but it is most likely that it was a combination of high egg mortality (due to lack of water) and high juvenile mortality. Egg mortality seems less probable for *Lacerta vivipara* at first glance, as the development of the eggs takes place within the body of the mother. For *K*-selected species the mother will first use the available resources for her own survival, which might lead to lower reproductive success in the short run. Patterson (1983) also mentions the negative influence of the dry year 1976 on the reproduction of *Anguis fragilis* in England.

A second effect of the drought in the summer of 1976 can be discerned in the figures for the reproductive success of the 3rd c.y. females of *Lacerta vivipara* in 1977 and of the 4th c.y. females of *Lacerta agilis* in 1978. Both year classes were subadults in 1976 and as a result of the extreme circumstances their growth was retarded in comparison with other years. In the *Lacerta vivipara* population of the Overasseltse and Hatertse Vennen Middelburg (1986) also found retarded growth in the subadults in 1976 and the

3rd c.y. animals in 1977, compared to normal years. As the third c.y. females of *Lacerta vivipara* have a large share of net reproduction (average 45.4%) the effect of low fractional participation of this year class in 1977 has a far greater impact on net reproduction than low fractional participation of the 4th c.y. females of *Lacerta agilis* in 1978.

As possible causes of mortality for lizards one could mention high water levels, fires, winter mortality, and predation. According to Bauwens (1981) and Lenders (1985) a high water level may also cause a high winter mortality. Inundation of hibernacula could not possibly take place in our test site. The only fire in the test site was a part of normal management rules and it took place on the northern slope in February 1976, when the lizards were still hibernating and therefore were not likely to be harmed by it. Bauwens (1981) mentioned exhaustion of fat reserves and frost as possible causes of death in *Lacerta vivipara*; however, this seems to apply especially to juveniles (12% winter mortality) and less to adults (0–8% winter mortality).

Predation might be one of the most important causes of mortality, especially in spring, as a result of the low temperatures and the slight covering of the soil resulting in fewer chances of escape. A predator that specialises on lizards is the smooth snake (*Coronella austriaca*) which also occurs at the test site.

The densities of *Lacerta vivipara* are rather low compared to those of some other populations. For these Pilorge (1981), Bauwens (1981), and Broers and Clerx (1981) give densities of respectively 200–300, 400–800 and 540/ha (without juveniles). Middelburg (1986) calculated for two test plots densities of 200 and 450/ha (without juveniles) in peak years. The biomasses calculated by us (average 0.84 kg/ha) are somewhat lower than those given by Pilorge (1981) and Broers and Clerx (1981) of 1.0 and 1.35 kg/ha respectively, though they are about the same as the values, calculated by Middelburg (1986) of 0.53 and 1.00 kg/ha in his two plots. When interpreting the data on densities and biomasses one should bear in mind that these are not evenly spread over the test site. In the transition zone to the forest densities and biomasses may be 2 or 3 times those on the rest of the test site.

The differences in densities and biomasses of the two species on the northern and southern slopes point to a spatial separation between them. *Lacerta vivipara* appears to concentrate especially on the northern slope. The differences in use of the terrain are largely due to differences in microhabitat between the two slopes. The northern slope is relatively moist and coverage of the soil by vegetation is high. The southern slope is drier and is characterised by a more open vegetation structure (Strijbosch 1986).

On the basis of life history strategies a distinction can be made between *r*- and *K*-selected species (Tinkle 1969). In the (sub)tropics and other regions with a long growing season are found mainly short-lived, *r*-selected species which reach sexual maturity very fast, are seldom viviparous, seldom show parental care, and have high juvenile and adult mortality. Therefore they allot much energy (and risk) to reproduction in the short run. These species produce more, larger clutches every year at the cost of their own survival. In more temperate regions with a relatively short growing season are found mainly long-lived *K*-selected species with later sexual maturity. As a rule they produce only one clutch per year and have low mortality. Relatively speaking they allot little energy and risk to reproduction in the short term but much to their own survival and parental care (Ballinger and Congdon 1981). These species are often viviparous, which might minimise the chances of reproduction failure (Tinkle 1969). On the other hand there is a larger chance of predation on account of greater immobility.

Lacerta vivipara and *Lacerta agilis* are good examples of *K*-selected, long-lived species with delayed sexual maturity, *Lacerta agilis* being the most *K*-selected of the two.

Not only within a genus but also within a species populations may have different life history strategies, as has already been shown for *Uta stansburiana* (Tinkle 1967) and *Sceloporus undulatus* (Tinkle 1972), among others, which turned out to be more *r*-selected in Texas than in the more northerly Colorado. For *Lacerta vivipara* our data were compared, as far as possible, with six other populations (see Introduction), so that these populations could be placed in an *r*-*K*-continuum. In doing so we took the following factors into account:

1. length of the active season
2. longevity
3. mortality
4. fecundity
5. minimum age at which sexual maturity is reached
6. the share of the younger year classes in the total net reproduction

A high score on factors 1, 3, 4, 5, and 6 and a low score on factor 2 indicate *r*-selection. The opposite scores indicate *K*-selection.

The Austrian mountain population (2200 m) is the most *K*-selected on account of the low mortality, high maximum age, and delayed sexual maturity, which is reached no sooner than in the fourth calendar year as a result of a very short growing season of only 4 months (Clerx and Broers 1982). The most *r*-selected may be the lowland population in Brittany, because 50% of the 2nd c.y. females already participate in reproduction, and no less than 62% of the total net reproduction is due to the 2nd and 3rd c.y. females (Heulin 1985a and b). In between these two extremes are the five other populations in which as a rule first reproduction by females is in the third calendar year. On the basis of the age structure and the rather high fecundity (5) of especially the 3rd c.y. females the French mountain population (1200 m, Pilorge and Xavier 1981) can be considered somewhat more *r*-selected than the four North Atlantic populations. The place of the British population is somewhat more difficult to define due to the absence of a life table and data on the share of the younger year classes in the total net reproduction. This population is characterised by high maximum age, large mean clutch size (Avery 1975b) and high fecundity (Avery 1975a) in the lower year classes. However, his calculations of theoretically attainable age and theoretical fecundity seem rather speculative, the more so because they are not supported by field data. These values suggest that this is the most *r*-selected of the four North Atlantic populations. The Belgian and the two Netherlands populations show only marginal differences in life history strategies. In the Hamert population the participation of the 3rd c.y. females in reproduction varies between 27% and 95% (average 56.3%), in the Belgian population for the years 1978–1981 between 52% and 100% (average 78.5%, see Bauwens 1985), while in the other Netherlands population an average of 86.7% was established over the years 1976–1980. In the period 1978–1981 the average participation of the 3rd c.y. females in the Hamert population was 79.3%, nearly equal to that of the Belgian population in those years.

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