Relationships between Maternal Size, Egg Size, Clutch Size, and Hatchling Size in European Lacertid Lizards

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ABSTRACT.—The interspecific relationships among female size, clutch size, egg size, and hatchling size were examined for 64 European lacertids. The eggs of all species increased linearly in both linear dimensions and mass during incubation. Across species initial egg mass was positively correlated with juvenile mass, with an allometric relationship exponent of 0.87. Initial egg mass across species increased proportionally with female mass to the power of 0.57. Moreover, an increase in maternal mass was also accompanied by an increase in clutch size. The number of eggs per clutch across species scaled with female mass to the power of 0.39. Removing the effect of female mass resulted in a negative correlation between egg mass and clutch size. Species for which the average egg size was lower than expected on the basis of female mass, tended to have larger relative clutch size. The total egg mass per clutch was about one third of female mass (exponent 0.94).

Although numbers of offspring per clutch are constant in geckos (Kluge, 1987; Werner, 1989), anoline lizards (Smith et al., 1973), and other groups of lizards (Shine and Greer, 1991), clutch size is more variable in European lacertids. Given that there is a finite quantity of energy available for a reproductive attempt, energy must be apportioned as few, large or as many, small offspring. The degree to which offspring number is compromised in favor of offspring size differs among species and for different populations of the same species living in different demographic environments. Furthermore, the annual quantity of energy available may be apportioned among a varying number of clutches.

The European lacertids form a group of closely related species occupying a large variety of habitats. Such a group is well-suited for the study of variation in a number of reproductive traits. Although reproductive traits of some species of lacertids have been studied (Castilla and Bauwens, 1989; Castilla et al., 1989; Van Damme et al., 1992) information on the number and size of eggs and juveniles is limited for most European lacertid lizards (Böhme, 1981, 1984, 1986). In this study we examined the relationships among female size, clutch size, egg size, and hatchling size for a variety of European lacertids. In reptiles in general, the relationship between egg mass and maternal body mass has an exponent of 0.57 (Blueweiss et al., 1978), suggesting a decrease of relative egg mass with body mass. If the same relative quantity of energy was available for all lacertids one may also expect an increase in clutch size with body mass. A trade-off between egg size and egg number present in single species (Van Damme et al., 1992) may also be present in the group of European lacertids. The study of life histories in a group of closely related species can lend insights into the life history evolution of individual species of these lizards.

MATERIALS AND METHODS

We collected data on reproductive characteristics of 64 West Palearctic lacertids between 1988–1992. All species were collected from the wild and kept in vivaria as part of a study investigating the courtship behaviour of these lizards by the first author. All species were kept in indoor terraria under a diel light regime approximating 42° latitude. Food (crickets, maggots, flies, mealworms), was supplemented by vitamins and minerals, and water were available ad libitum. Under the incandescent spots (25–40 W) substrate temperatures of maximally 45 C were reached. Ambient temperatures varied between 18–25 C. Most animals were hibernated for 3–5 mo (duration depending on the species) at temperatures of 3–5 C. The animals were normally kept in pairs, although sometimes two or three females were present in a terrarium.

Plastic boxes (11 × 11 × 6 and 13 × 17 × 6 cm) filled with moist potting soil provided a medium for oviposition and each box was checked daily. Several hours after oviposition, the eggs were removed from the plastic boxes, individually marked, and transferred to incubators maintained at a constant temperature of 25 ± 0.2 C or 29 ± 0.2 C and high humidity. Eggs were randomly distributed within the incubators. For the analyses of all egg and incubation variables only data for the 25 C regime were used. For hatchling mass, data were sometimes pooled within species after testing for differences in average mass (t-test). The water po-
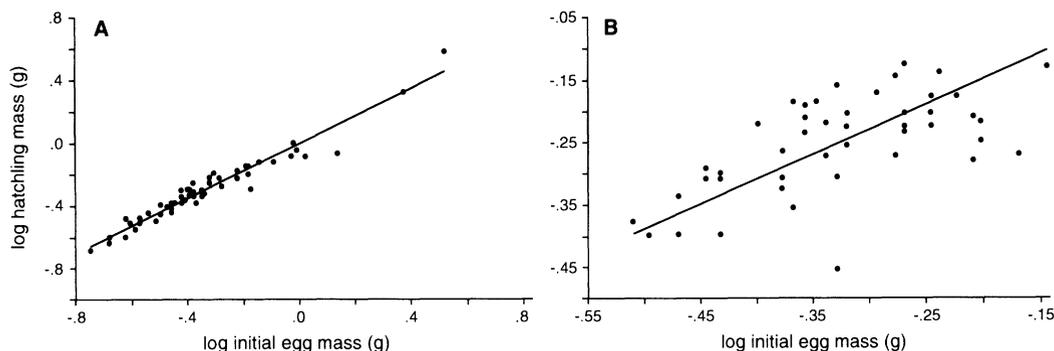
FIG. 1. (A) Relationship between initial egg mass (X) and hatchling mass (Y) for 57 species (Y = 0.97 $X^{0.87}$). (B) Relation between initial egg mass (X) and hatchling mass (Y) for 47 eggs of *Podarcis milensis* (Y = 1.00 $X^{0.78}$).

tential of the incubating medium was not recorded, although later measurements suggest a value between $-100/-400$ kPa. Eggs were regularly moistened with water using a plant spray bottle. Embryo mortality was low (10–15%) and eggs that failed to develop were excluded from the analyses. Mass was measured to the nearest 0.01 g using a Mettler balance. Temperatures were measured with a digital thermometer (±0.1 C) on the incubation substrate (synthetic aquarium filter material, Perlon). Egg width and length were measured to the nearest 0.1 mm using a digital calliper. Egg size measurements were obtained prior to the transfer to the incubator and subsequently at weekly intervals. Final linear egg measurements and mass were measured 1–2 d before hatching, when egg mass started to decrease and small droplets appeared on the surface of the egg.

Female mass was measured at the end of the summer, when females were not gravid. To characterize reproductive traits for each species, data were averaged over all females, clutches, and hatchlings within a species. Missing values sometimes precluded analysis of the full set of 64 species. For the analysis of egg or hatchling mass in relation to clutch size, average egg or hatchling mass per clutch was used.

RESULTS

Length, width, and mass of the eggs at oviposition and just prior to hatching, and snout–vent length, tail length, and juvenile mass are presented in Table 1. Egg size at oviposition varied from an average of 9.7 × 5.7 mm (0.18 g) in *Algyroides fitzingeri* to 19.8 × 14.5 mm (2.38 g) in *Lacerta lepida*. The eggs of all species increased in both size and mass during incubation. Before hatching, egg size increased to an average of 14.9 × 8.9 mm (0.75 g) in *A. fitzingeri* and to 28.5 × 19.5 mm (6.42 g) in *L. lepida*. In most of the lizards the relationship between egg mass and time was positive and linear. The rate of

increase of egg mass differed within and among species but this depended largely on initial egg mass.

Incubation duration at 25 C varied from 28 d for *Lacerta mosorensis* to 90 d for *Lacerta cappadocica schmidtlerorum*. The incubation period among species was positively correlated with female mass (r = 0.37; N = 53; $P < 0.01$) but this seemed to be due to the four largest species in the sample (>35 g). For the remaining species the correlation was not significant (r = 0.07; $P > 0.05$; N = 49). Initial egg mass and incubation duration were positively correlated (r = 0.50; $P < 0.01$; N = 58). Because data on *Lacerta* part I species (sensu Arnold, 1973) were limited we included observations from Bischoff (1981) on *Lacerta jayakari*. Without the large *L. lepida* and *Lacerta jayakari* the correlation between initial egg mass and incubation duration fell to r = 0.11 ($P > 0.05$; N = 56). Among species there was no correlation between the rate of increase of egg mass and the duration of incubation (r = 0.13; $P > 0.05$; N = 58).

For 57 species the average mass of the hatchling was 1.09 times larger than the average initial egg mass (Fig. 1A). Uptake of water through the porous flexible egg shell may explain the fact that hatchling wet mass is higher than initial egg mass (e.g., Kramer, 1938; In den Bosch, 1991). Egg mass and hatchling mass were correlated among species (r = 0.97). The exponent found for this relationship (hatchling mass = 0.97 × initial egg mass$^{0.87}$) is close to 1 and indicates that eggs of all sizes produce hatchlings with a mass proportional to egg mass. To test for this relationship within a single species, we assessed data for *P. milensis* for which a large number of measurements were available. Initial egg mass and hatchling mass was positively correlated (r = 0.58; N = 47; $P < 0.001$; Fig. 1B) and the exponent for this relationship (hatchling mass = 1.00 × initial egg mass$^{0.78}$) was similar to that found for the relationship across species.

TABLE 1. Egg dimensions and measurements on hatchlings. All measurements with standard deviations. Differences in total number of observations indicate missing measurements.

Species	Egg size										Hatchling size					
	At oviposition					Just before hatching					Just after hatching					
	Egg length	Egg width	N	Egg mass	N	Egg length	Egg width	N	Egg mass	N	SV length	N	Tail length	N	Mass	N
Algyroides																
A. fitzingeri	9.7 ± 0.8	5.7 ± 0.4	53	0.18 ± 0.03	65	14.9 ± 2.1	8.9 ± 0.5	36	0.75 ± 0.18	51	19.9 ± 1.1	51	33.3 ± 3.3	93	0.21 ± 0.02	73
A. marchi	10.6 ± 0.8	6.4 ± 0.6	63	0.27 ± 0.04	30	15.8 ± 1.7	9.8 ± 0.7	27	1.06 ± 0.13	22	22.0 ± 1.2	22	37.4 ± 2.9	42	0.31 ± 0.03	37
A. moreoticus	10.6 ± 1.0	5.9 ± 0.5	51	0.21 ± 0.07	40	15.1 ± 1.4	9.4 ± 0.6	58	0.80 ± 0.15	41	20.7 ± 1.2	41	35.9 ± 3.1	93	0.23 ± 0.04	61
A. nigropunctatus	11.4 ± 1.0	7.3 ± 0.5	39	0.32 ± 0.07	26	15.8 ± 1.9	11.2 ± 0.7	34	1.01 ± 0.18	21	22.4 ± 1.3	21	39.9 ± 4.4	41	0.35 ± 0.04	20
Gallotia																
G. atlantica	14.0 ± 0.5	8.5 ± 0.5	6	0.60 ± 0.07	6	20.9 ± 2.7	14.1 ± 1.0	5	2.43 ± 0.71	5	27.2 ± 0.8	5	55.2 ± 1.8	5	0.66 ± 0.02	5
G. g. eisentrauti	18.5 ± 0.6	12.5 ± 0.6	4	1.63 ± 0.13	4	21.0 ± 1.6	15.7 ± 1.0	4	3.13 ± 0.46	4	37.0 ± 0.8	4	90.7 ± 3.0	4	1.35 ± 0.09	4
Lacerta part I																
L. agilis	13.1 ± 0.3	9.0 ± 0.3	16	0.66 ± 0.04	16	18.2 ± 0.9	13.7 ± 0.4	6	1.79 ± 0.36	9	24.6 ± 5.1	9	41.5 ± 4.2	11	0.70 ± 0.05	6
L. lepida	19.8 ± 0.7	14.5 ± 0.3	12	2.38 ± 0.14	12	28.5 ± 1.1	19.5 ± 1.3	2	6.42 ± 0.67	2	36.5 ± 0.6	2	48.5 ± 4.9	2	2.09 ± 0.44	2
L. media	16.3 ± 0.6	12.2 ± 0.2	15	1.38 ± 0.05	15	24.1 ± 2.3	17.2 ± 1.0	4	3.97 ± 0.76	4	29.2 ± 1.3	4	48.8 ± 5.0	4	0.84 ± 0.13	4
L. cf. pamphylica	13.6 ± 0.5	8.9 ± 0.5	9	0.65 ± 0.06	9	19.2 ± 1.2	13.8 ± 0.7	9	2.07 ± 0.32	9	28.1 ± 1.2	9	51.1 ± 3.6	9	0.70 ± 0.05	9
L. schreiberi	13.5 ± 0.7	10.8 ± 0.4	17	0.94 ± 0.09	17	20.5 ± 1.1	15.8 ± 0.7	16	2.90 ± 0.37	16	28.3 ± 0.7	16	45.4 ± 6.6	16	0.80 ± 0.18	16
L. strigata	15.4 ± 0.9	10.7 ± 1.2	11	1.05 ± 0.26	11	22.1 ± 1.4	14.3 ± 0.2	8	2.68 ± 0.34	8	31.1 ± 1.6	8	53.0 ± 2.8	8	0.80 ± 0.04	8
Lacerta part II																
L. a. anatolica	11.9 ± 0.8	7.6 ± 0.5	15	0.41 ± 0.06	15	18.0 ± 1.2	11.8 ± 0.3	4	1.47 ± 0.15	4	22.5 ± 2.4	4	43.5 ± 2.1	4	0.50 ± 0.04	4
L. andreanszkyi	13.3 ± 0.7	6.3 ± 0.3	7	0.31 ± 0.03	7	15.3 ± 0.6	8.6 ± 0.2	6	0.70 ± 0.05	6	22.2 ± 1.1	6	34.3 ± 1.5	6	0.32 ± 0.03	6
L. armeniaca	11.7	7.4	1	0.38	1	16.8	11.4	1	1.32	1	25.0	1	24.0	1	0.41	1
L. b. bedriagae	16.2 ± 1.2	9.9 ± 0.5	17	0.98 ± 0.09	17	22.8 ± 1.8	14.7 ± 0.7	16	2.86 ± 0.30	16	32.3 ± 1.1	16	65.7 ± 5.7	16	0.88 ± 0.13	16
L. b. ferrerae	16.6 ± 1.0	9.6 ± 1.0	27	0.89 ± 0.09	27	21.5 ± 2.3	14.3 ± 0.7	16	2.48 ± 0.51	16	33.2 ± 1.4	16	61.1 ± 4.9	16	0.88 ± 0.16	16
L. cappadocica schmidtlerorum	11.6 ± 1.0	7.4 ± 0.4	53	0.38 ± 0.06	49	16.7 ± 1.3	11.3 ± 1.9	29	1.31 ± 0.18	29	24.9 ± 2.2	29	49.3 ± 4.4	38	0.50 ± 0.09	38
L. cappadocica cf. wolteri	13.3 ± 0.2	6.8 ± 0.2	5	0.38 ± 0.01	5	18.5 ± 1.7	10.1 ± 0.5	5	1.16 ± 0.19	5	23.8 ± 1.1	5	43.2 ± 4.2	5	0.41 ± 0.04	5
L. chlorogaster	10.4 ± 0.6	6.7 ± 0.1	15	0.29 ± 0.01	15	17.0 ± 2.6	10.9 ± 0.4	14	1.21 ± 0.32	14	24.4 ± 1.2	14	40.0 ± 2.3	14	0.35 ± 0.04	14
L. clarkorum	13.4 ± 0.4	7.5 ± 0.3	9	0.46 ± 0.03	9	17.8 ± 0.7	12.4 ± 0.4	12	1.53 ± 0.16	12	27.6 ± 1.2	12	49.1 ± 2.9	12	0.47 ± 0.06	12
L. daghestanica	11.4 ± 0.9	5.8 ± 0.2	13	0.26 ± 0.06	13	14.1 ± 1.0	8.8 ± 0.6	13	0.63 ± 0.11	13	22.7 ± 1.2	13	37.3 ± 3.6	11	0.28 ± 0.03	11
L. danfordi bileki	11.7 ± 0.7	7.1 ± 0.3	7	0.34 ± 0.05	7	18.0 ± 1.8	12.0 ± 0.7	6	1.50 ± 0.3	6	25.1 ± 0.7	6	46.3 ± 2.7	7	0.38 ± 0.07	7
L. d. danfordi	12.4 ± 0.5	7.4 ± 0.5	45	0.44 ± 0.03	14	17.5 ± 1.6	12.5 ± 1.5	30	1.57 ± 0.19	24	26.5 ± 1.1	24	52.5 ± 3.0	33	0.48 ± 0.05	33
L. derjugini cf. barani	10.7 ± 0.6	6.4 ± 0.2	41	0.25 ± 0.02	31	14.0 ± 0.9	9.6 ± 0.3	38	0.75 ± 0.09	38	22.9 ± 1.2	38	38.1 ± 1.9	38	0.31 ± 0.03	38
L. fraasii	13.0 ± 0.7	7.4 ± 0.1	5	0.42 ± 0.03	5	18.5 ± 1.5	10.8 ± 0.3	5	1.28 ± 0.06	5	22.4 ± 1.5	5	40.2 ± 3.9	5	0.48 ± 0.05	5
L. graeca	12.9 ± 0.6	8.1 ± 0.3	22	0.52 ± 0.03	8	19.4 ± 1.7	12.9 ± 0.4	18	1.83 ± 0.28	18	28.5 ± 1.8	18	55.6 ± 5.6	18	0.58 ± 0.05	18
L. horvathi	13.3 ± 1.3	7.4 ± 0.4	21	0.42 ± 0.06	21	17.4 ± 1.6	11.4 ± 0.4	19	1.30 ± 0.22	19	26.0 ± 1.2	19	43.9 ± 3.5	19	0.46 ± 0.10	19
L. laevis	11.4 ± 0.7	7.2 ± 0.3	43	0.35 ± 0.03	43	15.7 ± 1.1	11.0 ± 0.4	40	1.10 ± 0.12	38	25.4 ± 0.9	38	48.6 ± 4.5	48	0.41 ± 0.05	44
L. m. monticola	13.0 ± 1.0	7.1 ± 0.2	7	0.41 ± 0.05	7	16.5 ± 1.1	10.1 ± 0.3	7	1.03 ± 0.11	7	25.6 ± 1.0	7	40.6 ± 3.7	7	0.45 ± 0.07	7
L. mosorensis	15.6 ± 1.1	8.9 ± 0.6	6	0.67 ± 0.08	6	20.5 ± 1.8	10.8 ± 0.4	4	1.42 ± 0.17	4	25.7 ± 1.7	4	44.2 ± 1.5	4	0.50 ± 0.05	4

TABLE 1. Continued.

Column groups: **Egg size** — *At oviposition* (Egg length, Egg width, N, Egg mass, N) and *Just before hatching* (Egg length, N, Egg width, N, Egg mass, N); **Hatchling size** — *Just after hatching* (SV length, N, Tail length, N, Mass, N).

Species	Egg length	Egg width	N	Egg mass	N	Egg length	N	Egg width	N	Egg mass	N	SV length	N	Tail length	N	Mass	N
L. nairensis	12.3 ± 0.6	7.6 ± 0.3	11	0.42 ± 0.04	11	17.5 ± 0.8	11	10.8 ± 0.4	8	1.23 ± 0.12	8	27.4 ± 1.2	8	47.1 ± 2.7	8	0.46 ± 0.02	8
L. oertzeni ibrahimi	12.1 ± 0.8	6.9 ± 0.2	18	0.35 ± 0.03	18	18.6 ± 1.4	18	11.0 ± 0.7	14	1.34 ± 0.17	14	23.4 ± 1.9	14	47.4 ± 3.6	14	0.41 ± 0.05	14
L. oertzeni pelasgiana	11.9 ± 0.7	7.4 ± 0.4	19	0.38 ± 0.05	19	16.4 ± 1.0	10	12.0 ± 0.4	10	1.36 ± 0.15	10	26.4 ± 1.3	19	51.7 ± 2.2	19	0.49 ± 0.05	19
L. oxycephala	15.1 ± 1.3	7.6 ± 0.4	41	0.45 ± 0.04	41	18.2 ± 1.9	9	11.4 ± 0.6	14	1.25 ± 0.19	14	26.8 ± 1.7	14	48.6 ± 0.4	48	0.49 ± 0.07	48
L. parva	11.7 ± 1.0	7.1 ± 0.7	64	0.36 ± 0.05	54	17.8 ± 2.0	54	11.0 ± 0.9	55	1.27 ± 0.26	55	24.4 ± 1.6	55	41.3 ± 3.2	65	0.41 ± 0.06	65
L. parvula	13.5 ± 1.2	6.8 ± 0.5	21	0.35 ± 0.03	10	17.1 ± 1.1	10	9.9 ± 0.5	12	1.00 ± 0.16	12	25.5 ± 1.1	12	44.5 ± 2.8	8	0.36 ± 0.03	8
L. praticola pontica	10.5 ± 0.5	6.2 ± 0.3	42	0.24 ± 0.03	39	15.5 ± 1.5	39	10.0 ± 0.6	32	0.89 ± 0.14	32	22.1 ± 1.5	32	34.5 ± 3.2	53	0.25 ± 0.05	53
L. rudis obscura	14.4 ± 1.0	9.1 ± 0.5	14	0.66 ± 0.07	14	19.1 ± 1.8	14	12.8 ± 0.5	6	1.83 ± 0.28	6	27.9 ± 1.7	6	49.1 ± 4.9	13	0.62 ± 0.12	13
L. rudis 'Sivas'	12.4 ± 0.4	8.0 ± 0.1	8	0.45 ± 0.02	8	17.6 ± 0.3	8	11.6 ± 0.4	5	1.37 ± 0.07	5	27.5 ± 1.7	5	45.6 ± 3.7	8	0.48 ± 0.04	8
L. saxicola cf. brauneri	14.1 ± 0.5	7.7 ± 0.4	4	0.50 ± 0.05	4							26.0		47.0	1	0.49	1
L. unisexualis	12.3 ± 1.1	7.5 ± 0.3	15	0.42 ± 0.05	10	18.4 ± 2.0	10	11.4 ± 0.6	8	1.43 ± 0.28	8	27.0 ± 1.2	12	46.7 ± 3.0	12	0.49 ± 0.08	12
L. valentini	12.7 ± 1.6	7.5 ± 0.5	11	0.43 ± 0.10	11	17.6 ± 2.0	11	11.4 ± 0.4	14	1.34 ± 0.23	14	25.4 ± 1.3	14	41.6 ± 3.5	14	0.41 ± 0.10	14
L. vivipara						10.1 ± 0.6		7.2 ± 0.5	4	0.29 ± 0.02	4	17.9 ± 0.8	7	22.0 ± 1.8	8	0.17 ± 0.01	8
L. vivipara oviparous form						12.3 ± 0.8		9.1 ± 0.7	22	0.60 ± 0.07	22	20.5 ± 1.6	22	25.9 ± 1.4	21	0.24 ± 0.02	21
Ophisops																	
O. elegans	10.3 ± 0.7	5.6 ± 0.4	26	0.21 ± 0.02	13	17.0 ± 1.1	13	9.7 ± 0.9	10	0.98 ± 0.23	8	19.7 ± 0.8	6	34.3 ± 2.4	6	0.20 ± 0.02	6
Podarcis																	
P. bocagei	11.8 ± 0.7	6.8 ± 0.1	2	0.32	2	16.0 ± 0.9	2	10.8 ± 0.0	2	1.07 ± 0.07	2	25.0 ± 1.4	2	41.0 ± 1.4	2	0.40 ± 0.01	2
P. dugesii	15.9 ± 2.2	8.8 ± 0.9	32	0.81 ± 0.19	27	25.8 ± 1.9	27	14.3 ± 1.0	21	3.13 ± 0.51	21	30.5 ± 2.1	22	55.0 ± 4.7	22	0.74 ± 0.14	22
P. erhardii	14.7 ± 1.4	7.0 ± 0.6	4	0.48 ± 0.08	4	20.6 ± 1.1	4	14.0 ± 0.2	5	2.31 ± 0.19	5	27.8 ± 1.3	5	51.5 ± 2.7	5	0.60 ± 0.04	5
P. filfolensis	12.8 ± 0.7	7.8 ± 0.5	40	0.46 ± 0.07	28	19.8 ± 1.4	28	12.0 ± 0.6	21	1.65 ± 0.27	21	24.8 ± 2.8	21	45.5 ± 5.3	20	0.47 ± 0.05	20
P. hispanica	10.2 ± 1.1	6.3 ± 0.6	18	0.21 ± 0.02	18	15.4 ± 11.0	18	9.7 ± 0.5	14	0.82 ± 0.11	12	21.7 ± 1.5	15	33.5 ± 2.0	15	0.25 ± 0.04	15
P. lilfordi	14.3 ± 0.9	8.5 ± 0.5	22	0.60 ± 0.09	15	18.7 ± 1.5	15	12.9 ± 0.6	22	1.82 ± 0.26	22	28.7 ± 1.2	22	54.5 ± 3.0	21	0.58 ± 0.06	21
P. melisellensis	11.7 ± 0.4	7.2 ± 0.1	4	0.35 ± 0.02	4	18.0 ± 0.7	4	12.9 ± 0.7	3	1.75 ± 0.27	3	25.0 ± 1.0	3	43.7 ± 3.2	3	0.38 ± 0.03	3
P. milensis	13.3 ± 1.2	7.7 ± 0.5	89	0.48 ± 0.09	68	20.1 ± 2.4	68	12.1 ± 1.1	49	1.72 ± 0.45	47	26.1 ± 1.4	76	46.7 ± 4.1	76	0.55 ± 0.09	76
P. muralis	10.6 ± 0.7	6.8 ± 0.5	36	0.29 ± 0.05	28	15.7 ± 1.9	28	10.3 ± 0.4	28	0.98 ± 0.15	28	24.1 ± 1.1	28	37.3 ± 2.2	28	0.36 ± 0.04	28
P. peloponnesiaca	14.3 ± 0.5	7.7 ± 0.4	7	0.50 ± 0.06	7	20.1 ± 0.7	7	12.5 ± 0.7	12	1.97 ± 0.40	12	28.2 ± 1.5	12	49.5 ± 2.4	8	0.63 ± 0.06	8
P. perspicillata	13.7 ± 1.2	7.0 ± 0.5	35	0.38 ± 0.06	24	20.1 ± 4.3	24	12.1 ± 0.6	24	1.72 ± 0.31	26	25.7 ± 1.0	26	38.0 ± 2.4	22	0.45 ± 0.06	22
P. pityusensis	15.2 ± 1.2	9.0 ± 0.4	9	0.72 ± 0.08	9	21.7 ± 3.9	9	14.5 ± 1.9	9	2.70 ± 1.20	9	30.2 ± 1.5	9	56.5 ± 4.5	6	0.74 ± 0.12	6
P. sicula	11.3 ± 0.7	7.8 ± 0.3	18	0.40 ± 0.05	18	15.6 ± 3.7	18	11.5 ± 0.5	18	1.28 ± 0.15	18	25.1 ± 1.7	18	42.9 ± 4.9	14	0.50 ± 0.06	14
P. t. taurica	11.9 ± 0.7	7.7 ± 0.6	11	0.42 ± 0.07	11	19.3 ± 2.1	11	11.8 ± 0.7	9	1.56 ± 0.32	9	26.7 ± 1.5	8	48.5 ± 3.6	10	0.55 ± 0.08	10
P. tiliguerta	13.9 ± 0.6	7.6 ± 1.2	12	0.53 ± 0.06	12	21.4 ± 2.4	12	12.5 ± 1.6	8	2.00 ± 0.54	8	26.8 ± 1.9	12	51.4 ± 5.0	12	0.52 ± 0.10	12
P. wagleriana	12.2 ± 0.8	6.9 ± 0.4	12	0.34 ± 0.05	7	18.1 ± 2.1	7	11.4 ± 1.2	5	1.39 ± 0.39	5	26.2 ± 1.9	5	45.8 ± 3.3	5	0.46 ± 0.08	5
Psammodromus																	
E. algirus	11.9 ± 1.0	6.6 ± 0.5	8	0.27 ± 0.04	23	16.7 ± 1.9	23	9.9 ± 0.6	20	1.08 ± 0.18	20	25.5 ± 0.7	2	55.0 ± 14.2	2	0.56 ± 0.04	2
P. blanci	11.1 ± 1.1	6.2 ± 0.4	26	0.24 ± 0.04	29							21.5 ± 1.3	30	33.0 ± 2.6	30	0.33 ± 0.06	30
P. hispanicus	10.3 ± 0.6	6.3 ± 0.4	33			14.0 ± 1.4	29	10.5 ± 0.7	21	0.75 ± 0.10	12	22.6 ± 1.6	42	35.2 ± 3.2	42	0.33 ± 0.06	29
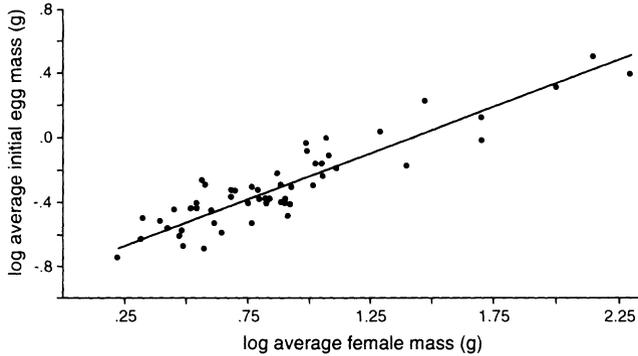
FIG. 2.   Relationship between log average female mass (X) and log initial egg mass (Y) for 57 species (Y = 0.15 $X^{0.57}$).

Female body mass was positively correlated with egg mass (r = 0.90; $P < 0.01$) and clutch size (r = 0.73; $P < 0.01$), which resulted in a positive correlation between clutch size and egg mass (r = 0.51; $P < 0.01$). Initial egg mass increased exponentially with female mass across species (exponent 0.57; Fig. 2). Clutch size scaled with female mass to the power of 0.39 (Fig. 3). The effect of female mass on the reproductive variables was removed by analyzing the differences between expected and measured values (allometric residuals) of both variables. The residuals of egg mass and clutch size were significantly and negatively correlated (Fig. 4; r = −0.52, N = 57, $P < 0.01$). Similarly, when female mass was held constant by partial correlation, clutch size and egg mass were negatively correlated (r = −0.47, N = 56, $P < 0.001$). Because egg mass and hatchling mass were positively correlated, a similar result was found for the relationship between clutch size and hatchling mass (r = −0.51, N = 56, $P = 0.001$). Therefore, species for which the average clutch size

was large relative to female body mass, also tended to have small relative hatchling size.

A similar negative correlation was found within species. Females of three species (*A. fitzingeri*, *A. moreoticus*, *P. milensis*) produced a sufficient number of clutches to analyze the relationships between egg size, clutch size, and hatchling size. Because the range of clutch sizes was small in most species and data were not bivariate normally distributed, Kendall's rank correlation was used (Table 2). In all three species clutch size was negatively correlated with both initial egg mass and hatchling mass. These data indicate that within species, large clutch size was associated with relatively small offspring size.

Total egg mass per clutch (TEC = average egg mass × average clutch size) was highly dependent on female mass (W) among species (Fig. 5; TEC = 0.29 $W^{0.94}$). The number of clutches per year per female did not correlate with species mass, egg mass, or clutch size.
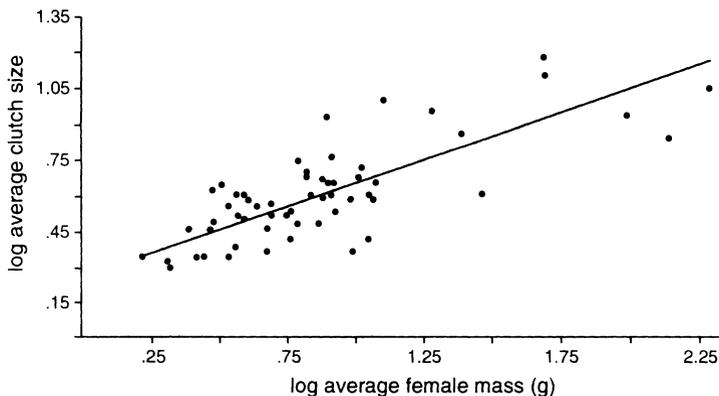
FIG. 3.   Relationship between log average female mass (X) and log average clutch size (Y) for 57 species (Y = 1.84 $X^{0.39}$).
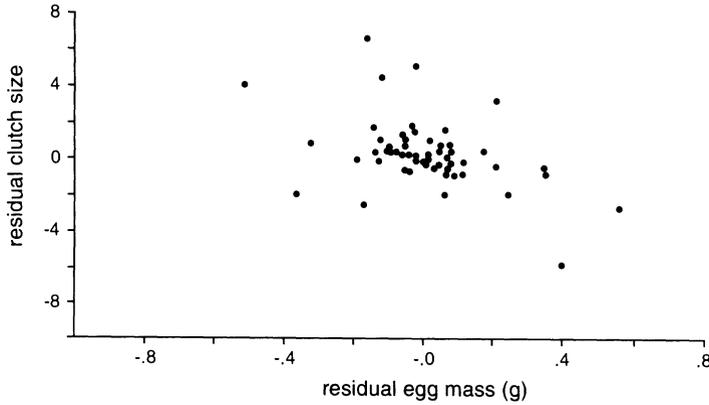
FIG. 4. Scatterplot of the difference between expected and measured egg mass and the difference between expected and measured clutch size (r = −0.448; N = 57).

DISCUSSION

We found that initial egg mass increased with body mass across our lacertid species. From our data it is clear that large species have relatively small eggs. The slope for the log transformed data (0.57) was much lower than in birds (Rahn et al., 1975) but somewhat higher than reported for reptiles in general (Blueweiss et al., 1978). Clutch size also increased with body mass. Both the analysis of allometric residuals and partial correlation analysis showed that, after removing the effect of body mass, there was a clear negative relationship between clutch size and egg mass. Across species the relationship between body mass and egg mass was stronger than the relationship between egg size and clutch size. As a result, both egg mass and hatchling mass increased with body mass.

The relationships between egg size, clutch size, hatchling size, and maternal body size within individual lacertid species are largely unknown. However, the basic relationship among these variables seem similar at species level. Within the three individual species investigated in our study, average egg mass decreased with increases in clutch size. A negative relationship was also found in *Podarcis muralis* (Van Damme et al., 1992) and in *L. lepida* (Castilla and Bauwens, 1989). This negative correlation between egg size and number is in agreement with a trade-off between egg numbers and egg size. Note however, that for the individual species our data are not corrected for female mass. In *P. muralis* (Barbault and Mou, 1988), *L. lepida* (Castilla and Bauwens, 1989), and *Lacerta vivipara* (Bauwens and Verheyen, 1987), clutch size increased with female snout-vent length (SVL). In snakes, a partial correlation analysis was used to eliminate the effect of female size from the relationship clutch size versus egg size (Ford and Seigel, 1989). Part of the decrease in average egg mass may therefore be the result of an increase in female size rather than clutch size per se. Our data on individual species were too limited and the range of body sizes too small to eliminate the effect of female mass, as was

TABLE 2. Relationships of clutch size and average egg mass, and average hatchling mass per clutch (g). Last column Kendall's rank correlation between the three variables and P-values.

Species	Clutch size (CS)	N	Average egg mass (EM)	Average hatchling mass (HM)	Correlation between		
					CS/EM P	CS/HM P	EM/HM P
A. fitzingeri	1	5	0.22 ± 0.04	0.25 ± 0.02	−0.329	−0.630	+0.433
	2	16	0.18 ± 0.02	0.20 ± 0.01	=0.05	<0.001	<0.01
	3	3	0.18 ± 0.01	0.20 ± 0.01			
A. moreoticus	1–2	5	0.26 ± 0.03	0.26 ± 0.01	−0.718	−0.680	+0.716
	3	8	0.21 ± 0.02	0.24 ± 0.03	<0.001	<0.001	<0.001
	4–5	4	0.18 ± 0.01	0.19 ± 0.01			
	4–6	12	0.32 ± 0.04	0.39 ± 0.07			
P. milensis	2	14	0.53 ± 0.01	0.58 ± 0.09	−0.669	−0.444	+0.491
	3	15	0.42 ± 0.06	0.52 ± 0.08	<0.001	<0.01	=0.001
	4	4	0.38 ± 0.01	0.46 ± 0.04			
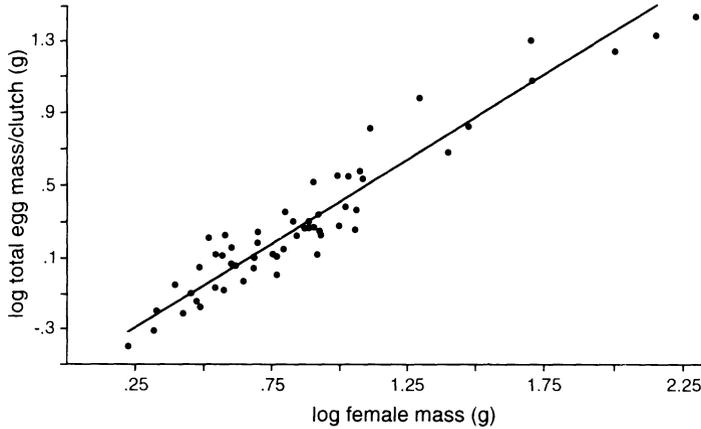
Fig. 5. Total egg mass per clutch (TEC: average initial egg mass multiplied by average clutch size) as a function of female mass (W) for 57 species (TEC = 0.29 W$^{0.94}$).

done with the partial correlation for all species combined. The individual species for which a sufficient range was available are summarized in Table 3. These data suggest that average egg mass and average clutch size remain more or less constant as females increase in size, but the number of clutches per year appeared to increase with female mass.

Phenotypic plasticity in clutch size of lizards has been found to be a response to proximate environmental conditions (James and Whitford, 1994). Temperature, hydric conditions, and maternal nutrition have been shown to influence incubation period, final egg mass, and hatchling size. Maternal nutrition may vary during the season and can affect egg size, egg number, and hatchling size (Ferguson and Bohlen, 1978; Nussbaum, 1981; Seigel and Ford, 1991). Eggs laid late in the season by *Sceloporus undulatus*

and *Uta stansburiana* are larger and produce larger hatchlings than do eggs laid earlier in the season. Such differences are not present in our data which may be a result of ad libitum availability of food and water throughout the year.

European lacertids are not, of course, an ecologically homogeneous group and several constraints may influence clutch mass and egg mass. It is generally assumed (Vitt and Congdon, 1978; Brodie, 1989) that females of widely foraging species have smaller relative clutch masses than do sit-and-wait females (Huey and Pianka, 1981) thus probably reducing predation risk. As the data of Perry et al. (1990) indicate, there could very well be a continuum of foraging modes in lacertid lizards which could complicate generalizations on reproductive traits in the European species. Moreover, Dunham et al. (1988) found a relationship between clutch size

TABLE 3. Relationships between individual female mass, average egg mass/clutch, average number of eggs/clutch, total number of clutches/year and total egg mass/year within a species.

Species	Female mass (g)	Average egg mass/clutch	Average eggs/clutch	Number of clutches	Total egg mass/year
A. moreoticus	2.16	0.13 ± 0.01	3.5 ± 2.1	2	0.91
	2.39	0.19 ± 0.03	3.3 ± 0.6	3	1.71
	2.53	0.19 ± 0.05	3.2 ± 0.8	5	3.04
	3.19	0.22 ± 0.05	3.5 ± 1.0	4	3.08
L. derjugini	3.78	0.25 ± 0.03	4.7 ± 1.2	3	3.52
	4.16	0.26 ± 0.01	3.0 ± 1.0	3	2.34
	4.44	0.22 ± 0.02	4.3 ± 0.6	3	2.84
L. laevis	5.45	0.35 ± 0.01	4.6 ± 1.2	3	4.83
	6.12	0.37 ± 0.02	5.3 ± 1.5	3	5.88
	6.89	0.34 ± 0.03	5.5 ± 1.9	4	7.39
L. parva	3.32	0.44 ± 0.07	5.0 ± 0.0	1	2.21
	3.78	0.36 ± 0.02	4.0 ± 1.0	3	4.27
	4.47	0.34 ± 0.02	5.5 ± 0.7	2	3.77
	4.53	0.36 ± 0.08	5.0 ± 1.4	2	3.65
	5.48	0.33 ± 0.01	5.2 ± 0.6	3	5.19

and habitat: arboreal and arenicolous lizards produced smaller clutches than terrestrial and saxicolous species.

The question remains to what extent trade-offs found for the group as a whole may be applied to individual species or populations. More data on individual species will have to be collected to test the relations described for the group. Furthermore, field data on individual offspring survival probability and the number of total surviving offspring are needed to give insight into the assumptions underlying optimal offspring size models.

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