# Effect of Relative Clutch Mass on Sprint Speed in the Lizard
## *Lacerta vivipara*

RAOUL VAN DAMME,1,2 DIRK BAUWENS,t.2.3.AND RUDOLF F. VERHEYEN/ ¹*Field Biologica/ Station, University of Antwerp (U.lA.), VerUindingsweg, B-2180 Kalmthout, Belgium;* ²*Department of Biology, University of Antwerp (U.l.A.), Universiteitsplein 1, B-2610 Wilrijk, Belgium.* ³*(Present Address: Research lnstitule for Nature Conservation, Kiewitdreef 3, B-3500 Hasselt, Belgium.)*

Relative clutch mass (RCM; the ratio of clutch to female body mass), a measure of the physical burden imposed on gravid females, is considered an important life history trait in reptiles. Several authors (Vitt and Congdon, 1978; Vitt, 1981; Vitt and Price, 1982; Seigel and Fitch, 1984) have hypothesized that RCM has evolved through differential mortality resulting from decreased locomotor ability and increased energetic costs of locomotion associated with transporting the added mass of the clutch.

Three lines of evidence support this hypothesis or its assumptions. First, comparative studies (Vitt and Congdon, 1978; Vitt and Price, 1982; Seigel and Fitch, 1984) have shown that high RCM values are found in lizards that do not rely on fast movement for foraging and escaping (sit-and-wait foraging, cryptic escape behavior), and in oviparous snakes; low RCM is associated with active foraging and fleeing escape behavior in lizards, and with viviparity in snakes. Secondly, intraspecific studies have shown a reduction of sprint speed (Shine, 1980; Bauwens and Thoen, 1981; Garland, 1985; Seigel et al., 1987) or endurance (Seigel et al., 1987) in gravid Jizards and snakes. Thirdly, differences among individuals in sprint speed and RCM have been identified in four scincid lizards (Shine, 1980) and one snake (Seigel et al., 1987). The Jatter studies strongly suggest that the added clutch mass exerts a direct negative effect on the locomotor performance of gravid females.

Inthis note we document the relation between sprint velocity and RCM in gravid females of the lizard *Lacerta vivipara.*

*Lacerta vivipara* is a small (adult body length: 45-65 mm) viviparous lizard that reproduces once a year. It is an agile lizard that forages actively on insects and other invertebrates (Avery, 1966; Itämies and Koskela, 1971; Koponen and Hietakangas, 1972; Pilorge, 1982), behaves like a typical heliotherm (Avery, 1976; Van Damme et al., 1987), and uses crypsis, flight and tail autotomy to escape from predators {Bauwens and Thoen, 1981). At parturition, this species has a remarkably high RCM (=clutch mass/female body mass after parturition). Mean values observed in different populations/years are: 0.81 (Bauwens and Thoen, 1981), 0.41-1.02 (Pilorge et al., 1983), 0.45-0.56 (Pilorge 1987) and 0.63 (this study). These values are among the highest reported for lizards in genera! ($i$ = 0.29; range 0.05-0.68) as well as in live-bearing species ($i$ = 0.31; range 0.13-0.48; recakulated from table 1 in Vitt and Price, 1982).

During April 1984, we captured adult female lizards in the Belgian national nature reserve "de Kalmthoutse heide" (51°25'N, 4°25'E, Province of Antwerp, Belgium). They were mated in the laboratory and maintained individually in outdoor enclosures until parturition.

About two weeks ($i$ = 14.9 days, range: 8-25) before parturition, we determined sprint speeds of 17 gravid and 6 nongravid adult females by chasing them by hand down a 2 m racetrack (Huey et al., 1981). The track was constructed of plywood with walls 30 cm high positioned 15 cm apart; its floor was covered with carpet that provided excellent traction. Nine pairs of photocells measured the time the lizards needed to cover 8 consecutive intervals of 25 cm. Before testing, we placed lizards in an incubator until their body temperature equalled 32.5°C (the optimum temperature for sprint speed in *L. vivipara* [Van Damme and Verheyen, 1987]). We tested each female once on each of 5 consecutive days. The fastest 25 cm interval of each trial was selected as an estimate of maximum sprint speed (Hertz et al., 1982). Sprint speed reported for each individual female is the average for the five trials. After the running experiments, females were weighed daily on an electronic balance (Mettler, precision = O.Dl g). We estimated clutch mass by the difference in female weight just before and after parturition.

Sprint speeds of gravid females ($i$ = 0.47 m/sec, SD = 0.12, N = 17) were significantly lower than those of nongravid ones ($i$ = 0.65 m/sec, SD = 0.11, N = 6) (t-test, $P < 0.01$). Mean snout-vent length of gravid females ($i$ = 5.73 cm, SD = 2.14, N = 17) was not significantly different from that of nongravid ones ($i$ = 5.65 cm, SD = 1.79, N = 6) (t-test, $P > 0.05$), so differences in sprint speeds seem not due to size differences. A two-way ANOVA on the gravid female group revealed significant differences between trials ($F$ = 3.7, $P < 0.01$) and between individual females ($F$ = 6.1, $P < 0.001$). Running performance was highest in the first trial, gradually decreased to a minimum in the fourth trial, and was higher again in the last trial. lndividual repeatability between trials was very high (Kendall coefficient of concordance W = 0.8, $P < 0.001$) (see also Bennett, 1980; Hertz et al., 1982; Crowley, 1985; Garland, 1985). A strong negative correlation was evident between sprint speed and RCM in individual females (Fig. 1, $r = -0.73, P = 0.001$).

Our results confirm those of Bauwens and Thoen (1981): pregnancy is associated with a reduction of sprint speed in this lizard. In addition, we here show that interindividual differences in running speed are related to RCM. Such a relationship has previously been established in four lizards (Shine, 1980) and one snake (Seigel et al., 1987). Our results hence seem to provide further support to the supposition that the mass of the dutch affects locomotor abilities in female reptiles. We should include here a note of caution in the interpretation of our results and those of Shine (1980) and Seigel et al. (1987). *As* differences in sprint speed at distinct reproductive stages were not examined at the individual level, the possibility remains that the relation between speed and RCM is an artefact. Individual variation in running performance,
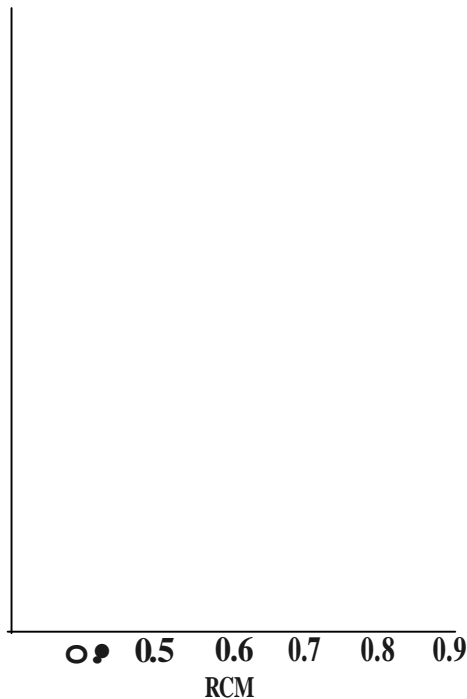
0.5    0.6    0.7    0.8    0.9
RCM

FIG. 1. Correlation between relative clutch mass (RCM) and sprint speed in female *Lacerta uiuipara.*

irrespective of reproductive characteristics, has been reported for a variety of lizards, including *L. uiuipara* (Huey, 1982; Huey and Hertz, 1982; Hertz et al., 1983; Crowley, 1985; Garland, 1985; Marsh and Bennett, 1986; Huey and Dunham, 1987; Van Berkum and Tsuji, 1987; Van Damme and Verheyen, 1987).

In female *L. uiuipara,* the reduction of locomotor abilities associated with pregnancy and increasing RCM values, might influence functions such as foraging, escape from predators and thermoregulation, which all involve (rapid) displacements. If success of these functions is dependent on running speed, selection should tend to reduce RCM. Hence, the high RCM observed in this lizard is rather surprising. It should however be noted that these RCM values were determined at parturition. At that time, RCM probably obtains its maximum value during the course of the reproductive season, because: (1) clutch mass increases owing to water uptake by the embryos (Xavier, 1984); and (2) body mass of females decreases, especially during the last 2-3 weeks of pregnancy (Bauwens and Verheyen, 1985; Bauwens, unpubl. obs.). Therefore, RCM values in this lizard might not be directly comparable with those reported for other species. Nevertheless, we are confident that RCM in *L. uiuipara* is high compared with those of other Jizards, as illustrated by the marked distension of the body in gravid females. In addition, running speed was inversely correlated with RCM in individual Jizards, suggesting that females carrying a heavy clutch are at a selective disadvantage. This result, together with the high RCM values, might indicate that the link between running performance and fitness is indirect in female L. *uiuipara.* Several hypotheses might be formulated in this respect.

First, sprint speed might not be very important in

this lizard. This argument might be just i.fied by the low maximum sprint speeds in male *L. viuipara* compared with those of other lizards of comparable size (Van Damme and Verheyen, 1987). Also, this lizard lives in densely vegetated habitats that may reduce the need to run over large (>2 m) distances to escape from predators or pursue prey.   ·

Secondly, females seem to compensate for reduced locomotor capacities by changing several aspects of their behavior. These include: (1) a lowered displacement rate as shown by the relative small home-range size of gravid females (D. Bauwens and S. Masure, unpubl. obs.); (2) a shift in predator escape behavior from active flight towards crypsis (Bauwens and Thoen, 1981) and (3) a reduction of the selected and field body temperatures (Patterson and Davies, 1978; Van Damme et al., 1986; Heulin, 1987), which may diminish the necessity to perform shuttling thermoregulatory displacements. These behavioral shifts might be such that decrements in running speed resulting from carrying a heavy clutch have little or no effect on fitness.

Thirdly, factors that tend to increase RCM might be more important determinants of fitness, or at least outweigh the costs induced by lowered locomotor capadties. The high RCM in this live-bearing lizard is induced by the production of a single annual, relatively large clutch, and the carrying of the clutch until its full development. It has been argued that these reproductive habits are at a selective advantage at high latitudes, where the short breeding season leads to single-broodedness (Tinkle, 1969; Tinkle and Gibbons, 1977) and cold climatic conditions favour egg-retention or viviparity (Shine, 1983).

These considerations accentuate the need for studies examining the relationship between reduced locomotor performance and survival abilities in natural populations of reptiles (see also Bauwens and Thoen, 1981; Seigel et al., 1987).

l..rrERATURE CITED

AVFJl..Y, R. A. 1966. Food and feeding habits of the common lizard *(Lacerta uiuipara )* in the west of England. J. Zool. (Lond.) 149:115-121.

—.   1976. Thermoregulat ion, metabolism and social behaviour in Lacertidae. *In* A. d'A Bellairs and C. B. Cox (eds.), Morphology and biology of reptiles, pp. 245-259. Linnean Society Symposium, Ser. 3. London.

BAUWENS, D" AND C. THOEN. 1981. F.scape acties and vulnerability to predation associated with reproduction in the lizard *Lacerta viuipara.* J. Anim. Ecol. 50:733-743.

AND R. F. VERHEYEN . 1985. The timing of reproduction in the lizard *Lacerta uiuipara:* differences between individual females. J. Herpetol. 19: 353-364.

BENNETT, A. F. 1980. The thermal dependence of lizard behaviour. Anim. Behav. 28:752-762 .

CROWLEY, S. R. 1985. Insensitivity to desiccation of sprint running performance in the lizard, *Sceloporus undu/atus.* J. Herpetol. 19:171-174.

GARLAND, T. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. J. Zool. (Lond.) 207:425-439.

HERTZ, P. E., R. B. HUEY, AND E. NEVo. 1982. Fight versus flight: body temperature influences defensive responses of lizards. Anim. Behav. 30:676-679.

—, —, AND —. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. Evolution 37:1075-1084.

HEULIN, B. 1987. Température diurne d'activité des males et des fémelles de *Lacerta vivipara*. Amphibia-Reptilia 8:393-400.

HUEY, R. B. 1982. Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. Koedoe 25:43-48.

—, AND A. E. DUNHAM. 1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. Evolution 41:1116-1120.

—, AND P. E. HERTZ. 1982. Effects of body size and slope on sprint speed of a lizard *(Stellio (Agama) stellio)*. J. Exp. Biol. 97:401-409.

—, W. SCHNEIDER, G. L. ERIE, AND R. D. STEVENSON. 1981. A .field-portable racetrack and timer for measuring acceleration and speed of small cursorial animals. Experientia 37:1356-1357.

ITÄMJES, J., AND P. KosKELA. 1971. Diet of the common lizard *(Lacerta vivipara* Jacq.). Aquilo Ser. Zool. 11:37-43.

KOPONEN, S., AND H. HIETAI<ANGAS. 1972. Food of the common lizard *(Lacerta vivipara* Jacquin) on a peat bog in southwestem Finland. Ann. Zool. Fenn. 9:191-192.

MARsH, R. L., AND A. F. BENNETT. 1986. Thermal dependence of sprint performance of the lizard *Sceloporus occidentalis*. J. Exp. Bio!. 126:79-87.

PATTERSON, J. W., AND P. M. C. DAVIES. 1978. Preferred body temperature: seasonal and sexual differences in the lizard *Lacerta vivipara*. J. Therm. Bio!. 3:39-41.

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

——. 1987. Density, size structure, and reproductive characteristics of three populations of *Lacerta vivipara* (Sauria: Lacertidae). Herpetologica 43:345-356.

——, F. XAVIER, AND R. BARBAULT. 1983. Variations in litter size and reproductive effort within and between some populations of *Lacerta vivipara*. Holarct. Ecol. 6:381-386.

SEIGEL, R. A., AND H. S. FITCH. 1984. Ecological patterns of relative clutch mass in snakes. Oecologia (Berl.) 61:293-301.

—, M. M. HUGGINS, AND N. B. FORD. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. Oecologia (Berl.) 73:481-485.

SHINE, R. 1980. "Costs" of reproduction in reptiles. Oecologia (Berl.) 46:92-100.

——. 1983. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. Oecologia (Berl.) 57:397-405.

TINl<LE, 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 J. W. GIBBONS. 1977. The distribution and evolution of viviparity in reptiles. Mise. Pub!. Mus. Zool. Univ. Mich. 154:1-55.

VAN BERKUM, F. H., AND J. S. ÎSUJI. 1987. lnter-familiar differences in sprint speed of hatchling *Sceloporus occidentalis* (Reptilia: Iguanidae). J. Zool. (Lond.) 212:511-519.

VAN DAMME, R., D. BAUWENS, AND R. F. VERHEYEN. 1986. Selected body temperatures in the lizard *Lacerta vivipara:* variation within and between populations. J. Therm. Biol. 11:219-222.

—, —, AND —. 1987. Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. Herpetologica 43:405-415.

—, AND R. F. VERHEYEN. 1987. Parameters in the thermal ecology of the common lizard, *Lacerta vivipara*. In J. J. van Gelder, H. Strijbosch, and P. J. M. Bergers (eds.), Proceedings of the Fourth Ordinary Genera! Meeting of the Societas Europaea Herpetologica, pp. 415-419. Faculty of Sciences, Nijmegen, The Netherlands.

Vm, L. J. 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. Am. Nat. 117:506-514.

—, AND J. D. CoNGDON. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. Amer. Natur. 112:595-608.

——, AND H. J. PRICE. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. Herpetologica 38:237-255.

XAVIER, F. 1984. Développement embryonnaire et flux transplacentaires d'eau chez *Lacerta vivipara* Jacquin. In R. Barbault and T. Pilorge (eds.), Ecologie et physiologie du lézard vivipare, 19. Ecole Normale Supérieure, Paris.