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Clutch Size and Reproductive Effort in the Lizard *Lacerta vivipara* Jacquin

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Summary. The ratio clutch weight: body weight in *Lacerta vivipara* is 0.4; larger lizards produce more eggs, and total clutch weight is isometric with body weight. The clutch represents between 7% and 9% of the estimated annual assimilation of a female lizard, and 23–24% of the assimilation during the period between emergence from hibernation and the establishment of the eggs in the oviducts.

Energy budgets of animals have received increasing attention in recent years. One feature of such budgets which has been examined in detail is the way in which the energy available to the individuals of a species is apportioned between reproductive and other activities (Williams, 1966; Pianka, 1970). Lizards have been studied from this point of view by Tinkle (1969) and Tinkle *et al.* (1970).

Lacerta vivipara Jacquin is of considerable interest because it occurs in cool temperate climates rather than in the warmer subtropical and tropical areas with which lizards are usually associated, and in which they have been most commonly studied. In Britain, adult females produce annually one clutch, which is retained in the oviducts until the eggs are ready to hatch. This paper examines the relationship between the food energy available to an adult female lizard in the field, and the energy cost of producing the clutch.

Materials and Methods

50 adult female lizards were captured between April 29 and July 20 in 1969–1971 and 1973, at Priddy in Somersetshire or Winsley in Wiltshire (U.K.). These habitats are described by Avery (1966). The lizards were stored in deepfreeze, to be thawed and dissected later.

The total and snout-vent (*S-V*) lengths of each lizard were measured with a pair of dividers. The tail was then cut off at the cloaca and the eggs were removed. In well-developed eggs the embryo was separated from the surrounding membranes. All of these parts of the body were dried at 65° C and weighed. The eggs from one oviduct were then used for determination of nitrogen, using standard semi-micro Kjeldahl procedures, and those from the other oviduct were used for lipid determination in a Soxhlet apparatus using hot chloroform as solvent. Total nitrogen and lipid in each clutch were calculated from the relative weights of the two groups of eggs. A further series of lizards were captured in March (males) or April (females), June and September, and was used for determination of carcass nitrogen. Determinations were by semi-micro Kjeldahl digestion of samples of approximately 30 mg of dried homogenised tissue.

In order to determine feeding levels, a colony of lizards was kept in an open vivarium on the roof of the Zoology Department building from 1969–1971, and emergence and feeding behaviour were recorded daily. Each day was assigned to one of the three categories: "sunny", on which emergence took place in the early morning (see Avery and McArdle, 1973) and feeding was normal; "changeable", which were those days on which emergence was later and feeding

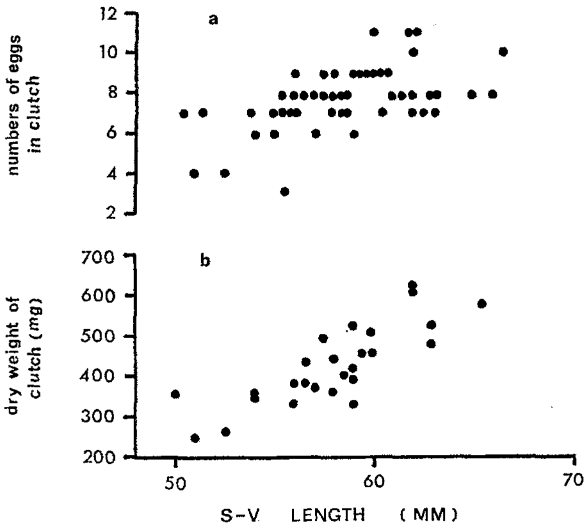

Fig. 1. (a) Number of eggs in the clutch, and (b) dry weight of the clutch, in relation to *S-V* length

was sporadic; and "dull" days were those on which there was no feeding, and often no emergence. Emergence from and returns to the burrow in the vivarium were recorded visually whenever possible, and they were also recorded automatically using a light beam and light sensitive cell at the entrance to the burrow; the passage of lizards was recorded on a kymograph drum with an accuracy of ± 10 min. When direct observations were not possible, feeding activity was assessed from the emergence and retreat times recorded on the kymograph.

Results

Clutch Size

The number of eggs dissected from 50 pregnant lizards ranged from 3–11, with a mean of 7.74. The biggest clutches were in the largest lizards; this is shown in Fig. 1a, in which egg numbers have been plotted against snout-vent length ($r = 0.54$, $P < 0.001$).

In order to determine the relation of the weight of each clutch to other body measurements, it was necessary to restrict the analysis to those clutches dissected after the eggs had established in the oviducts, since until this time they are increasing in weight, but also to restrict it to the period before embryonic development had proceeded to an advanced stage. This period has been taken as May 26 to June 15 (see Fig. 2). 26 such clutches were available.

The total dry weight of these clutches increased with *S-V* length (Fig. 1b) and *S-V* dry weight; the regression for the latter relationship is

$$C = 0.69\,W^{1.09}. \qquad (1)$$

Clutch weight is hence directly proportional to body weight. The mean dry weight of the eggs in a clutch was constant, irrespective of the size of the clutch ($r = -0.27$, $P > 0.1$); the increase in clutch weight with body weight is hence due to increasing egg numbers, and not to change in egg size.

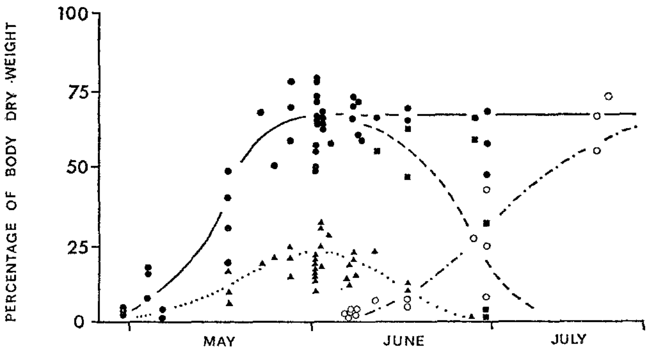

Fig. 2. Changes in the weight of the clutch (•——•), the yolk where this is a fraction of the total (▪----▪), lipid (▴·····▴) and the embryo (o-·-o). All weights are expressed as percentages of the body (snout-vent) weight. The curves are fitted by eye

The Constitution of the Clutch

The eggs are initially composed almost entirely of yolk, approximately 30% of which is chloroform-soluble lipid, and 8% is Kjeldahl nitrogen. Development of the embryo begins in June, and from this point the embryo grows rapidly at the expense of the yolk. Changes in the relative weights of yolk, lipid, and embryo are shown in Fig. 2; in order to reduce the variation due to differences in the sizes of individual lizards, all weights are expressed as percentages of the *S-V* dry weight. The total dry weight of the eggs in a clutch, and their total nitrogen content, remains constant after they have been transferred to the oviducts at the end of May.

Reproductive Effort in Relation to the Availability of Energy, Nitrogen and Lipid

It can be seen from Eq. (1) that the fully developed clutch weighs more than half of the *S-V* body weight of an adult female lizard; it comprises 40% of the total weight (*i.e.* including the tail). A lizard weighing 1 g dry weight, which is equivalent to 3.4 g live weight, must synthesize 400 mg of yolk; 120 mg of this is lipid and 32 mg is Kjeldahl nitrogen. It is of interest to compare these quantities with the inputs to the animal as assimilation.

It was shown by Avery (1971) that the daily food intake by *L. vivipara* was dependent upon the weather, and in particular upon amounts of solar radiation. Equations were given showing the mean food consumption on "sunny" and "changeable" days; feeding did not occur on a third category of days, called "dull". Provided that the total number of such days is known, the overall food consumption in any period can be calculated. Fig. 3 shows the number of days in each category in 1969, 1970 and 1971. The consumption of food in each year (C) has been calculated from this data, and converted to assimilation (A) from the relation

$$A = C - [(C - 0.89C) + (C - 0.93C)]$$

to allow for material egested (Avery, 1971) and material excreted (Avery, unpublished data). The results are shown in Table 1. Assimilation of nitrogen has

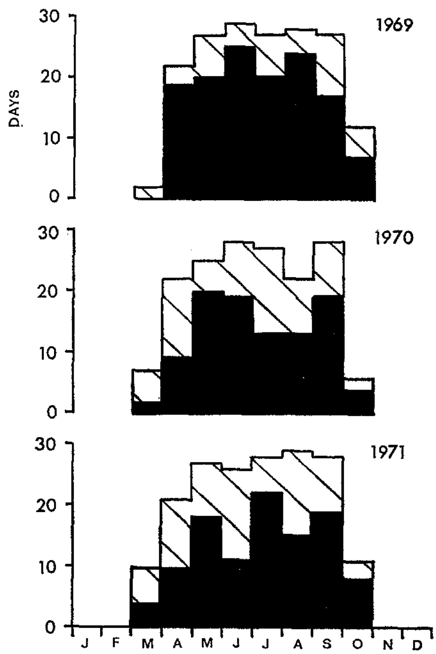

Fig. 3. Monthly totals of 'sunny' (black) and 'changeable' (hatched) days in 1969, 1970 and 1971. For definitions see text

Table 1. Calculated assimilation of food and nitrogen by a 3.4 g female lizard (a) over the whole year, and (b) during the period between emergence from hibernation in early March and May 25, in the years 1969–1971

	(a) Whole year		(b) To May 25	
	Food (mg)	Nitrogen (mg)	Food (mg)	Nitrogen (mg)
1969	5782	457	1415	115
1970	4377	356	1185	108
1971	4687	415	1128	99

been calculated in a similar manner, on the additional assumptions that the diet comprises 50% spiders and 50% Homoptera (Avery, 1966), that these have nitrogen contents of 13% and 9.6% respectively (Avery, 1971), and that 54.6% of ingested nitrogen is excreted as uric acid (unpublished data).

Table 1 also shows similar calculations of the assimilation during the period between emergence from hibernation in early March and May 25, which is the approximate data on which the eggs cease growing because they transfer to the oviducts (Fig. 2). All the calculations in Table 1 are for an adult female lizard with a S-V dry weight of 700 mg. Such an animal would have a total dry weight (*i.e.* including the tail) of about 1 g, a total live weight of about 3.4 g, and a *S-V* length of 60 mm. It can be seen from these figures that the clutch represents 7.9% of the annual assimilation during the spring period when most synthesis occurs, and the nitrogen requirement is equivalent to 27–32% of the spring assimilation.

Food is not the only source of energy for synthetic processes in the spring, since lipids from the abdominal fat bodies and the deposits between the epaxial muscles of the tail and the caudal vertebrae are mobilised at this time. A 60 mm female lizard loses 205 mg of lipids from these deposits between March 1 and May 25 (Avery, 1974, Figs. 1 and 2). This is nearly double the quantity in the clutch. If it is assumed that the lipid fraction of the yolk is derived entirely from the fat deposits, then the weight of the remaining material in the clutch represents only 10.5% of the spring assimilation.

The clutch is not produced at the expense of body nitrogen, which remains constant at 7.3–8.4% of the dry weight throughout the year (t for differences in mean nitrogen content of males and females in March–April, June and September was in all cases not significant, $P > 0.1$).

Discussion

The ratio clutch weight: body weight in *L. vivipara* is 0.4; this is at the upper end of the normal range for lizards, based on an examination of fourteen species, which is 0.1–0.4 (Tinkle, 1969). Many of these species, however, produce more than one clutch per year. In the Japanese Lacertid *Takydromus tachydromoides* the weight of an individual clutch varies from 30% to 50% of the body weight (Telford, 1969). Clutch weight is directly proportional to body weight in *L. vivipara*; the size of the clutch does not, therefore, explain the marked positive allometry in the size of the lipid stores in this species (Avery, 1974).

The relative proportions of lipid and Kjeldahl nitrogen are similar to those reported in the yolk of *Anolis carolinensis* by Hahn and Tinkle (1965), and the amounts of these materials invested in a clutch are approximately the same in both species. *A. carolinensis* produces only 4 eggs per clutch, so the individual eggs are larger, but it produces more than one clutch per year, so the annual investment in reproduction is greater.

It is not possible to compare the relation between assimilation and reproductive effort with other data for lizards, because there is no other species in which both of these parameters have been measured with sufficient precision. In a very detailed study of the salamander *Desmognathus ochrophaeus*, Fitzpatrick (1973) showed that vitellogenesis represents 32% of the annual energy assimilation. This is very much higher than the equivalent figure for *L. vivipara* (7–9%). The difference may in part reflect the fact that the salamander has a lower life expectancy; a female *D. ochrophaeus* at the time of first spawning has a life expectancy of less than 2 years (Tilley, 1970), whereas *L. vivipara* at a similar time has an expectancy of 3–4 years (Avery, 1975). The production of a clutch of eggs does not result in a metabolic drain on the female *L. vivipara* of the kind that is seen in many species of fishes (Love, 1970). Body nitrogen is much depleted in 'spent' fish, but in *L. vivipara* it remains constant. It is not known whether any minor nutrients are limiting; a high calcium demand might be expected in some lizards, but not in ovoviviparous species such as *L. vivipara*.

It should be noted that the estimates of reproductive effort refer only to the potential energy of the completed clutch. The metabolic cost of synthesizing the materials is not known.

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