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CLUTCH AND EGG SIZE IN LADYBIRD BEETLES

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There was a significant positive correlation between the number of ovarioles and clutch size in the 8 species of cocinellid studied. There was no intraspecific correlation between egg size and clutch size under standard conditions. These tactics are discussed in terms of the allocation of resources to reproduction.

KEY-WORDS : Coccinellids, egg size, clutch size, ovariole number.

Recently much interest has been shown in insect reproductive tactics (e.g. **Godfray,** 1987 ; **Mangel,** 1987 ; **Parker & Courtney,** 1984) and it has been demonstrated that there is a trade-off between egg size and clutch size (**Parker & Begon,** 1986), that is, a given reproductive effort may be invested in producing either a few large eggs or many small ones.

For any one individual the allocation of reproductive resources takes place in 2 stages. Firstly the maximum clutch and egg size are subject to anatomical and physiological constraints, since it is not possible to lay an egg larger than the ovariole in which it develops, nor is it possible to lay a greater number of eggs than is dictated by the rate of ovum synthesis. These factors are of course subject to natural selection and in this way an individual's maximum potential reproductive output is fixed through the partitioning of body mass between soma and gonads during early development. Whether or not this reproductive potential is realized will depend on environmental factors such as food supply. Secondly, selection acting through behaviour, may operate during the egg laying period. Here the decision is whether to lay eggs smaller than the maximum size (if this is not a fixed attribute) and how to apportion the available resources between clutches.

This paper is concerned with both of these processes, in that it examines the interspecific relationship between ovariole number and clutch size for several cocinellid species and the intraspecific relationship between egg and clutch size for 4 species of ladybird beetles.

MATERIALS AND METHODS

CLUTCH SIZE

Sixty pairs of *Adalia 10-punctata* (L.), *Hippodamia conglobata, H. convergens* Guerin, *Harmonia axyridis* Pallas and *Olla v-nigrum* (Mulsant) were reared in the laboratory during the months of May to September. A natural photoperiod was used, temperatures ranged from 18 °C (min) to 29 °C (max), and humidity was in the range 40-90 % R.H. The coccinellids were fed a number of different species of aphid but mostly *Myzus persicae* (Sulzer) and *Acyrthosiphon pisum* (Harris). The clutches of eggs were removed and counted daily.

In the case of *Coccinella trifasciata* L. 12 pairs were reared at 22 °C and fed *A. pisum*. Only those clutches of which 50 % or more of the eggs hatched were used to determine average clutch size.

EGGS FROM DIFFERENT SIZED CLUTCHES

(a) *A. bipunctata* (L.), *A. 10-punctata, P. 14-punctata* (L.)

The number of eggs in each of 13 clutches for *A. bipunctata* and *A. 10-punctata* and in each of 11 clutches for *P. 14-punctata* was determined with the aid of a hand lens (× 4). Eggs were weighed individually on a Cahn microbalance. Owing to the time consuming nature of removing them intact from the paper on which they were laid, the mean of 3 eggs chosen at random was taken as the mean egg weight for the clutch.

(b) *C. trifasciata*

Egg batches that had been laid on a double thickness of paper were cut out so that a duplicate area of paper existed, and the weight of the batch could be calculated from weight of clutch plus paper minus weight of duplicate piece of paper. The weight of each clutch was divided by the number of eggs to give the mean egg weight.

RESULTS

OVARIOLE NUMBER AND CLUTCH SIZE

Table 1 summarizes the results obtained both in this study and those in the literature. There is a strong positive correlation between the number of ovarioles and clutch size ($r = 0{,}89$), which is described by the following regression equation (1).

$$\text{Clutch size} = 0.54 \text{ Ovariole number} - 2.2. \quad (1)$$

Thus, species with a large number of ovarioles lay larger clutches than species with few ovarioles (fig. 1). The average clutch size of a species is approximately equal to half the number of ovarioles.

EGG SIZE AND CLUTCH SIZE

Table 2 indicates that for the 4 species of coccinellid examined there was no significant correlation between egg size and clutch size. Under the standard experimental conditions used there was no intra-specific trade-off between egg size and clutch size, with egg weight varying little between small and large clutches. Thus, egg size can be regarded as a species specific characteristic.

DISCUSSION

The number of ovarioles sets an upper limit to the number of eggs that can be produced in any one clutch when food is abundant. In the 11 species of coccinellid studied, the actual

TABLE 1
The number of ovarioles and clutch size of 11 coccinellid species (S.E. in parenthesis)

Species	Median number of ovarioles	Author	Mean clutch size	n
Adalia bipunctata	46	Iperti (1965)	30 (Iperti)	
Propylea 14-punctata	24	—	12 (Iperti)	
Coccinella 7-punctata L.	87	—	50 (Iperti)	
Adonia variegata (Goeze)	42	—	20 (Iperti)	
Adonia 11-notata	57	—	30 (Iperti)	
Adalia 10-punctata	20	Dobzhansky (1924)	10.6 (5.9)	468
Hippodamia conglobata	24	—	4.7 (3.3)	516
Harmonia axyridis	66	—	27.4 (15.4)	293
Hippodamia convergens	24	Williams (1945)	19.2 (10.5)	67
Olla v-nigrum	55	Kreiter (1985)	27.1 (14.1)	356
Coccinella trifasciata	42		10 (4.05)	38

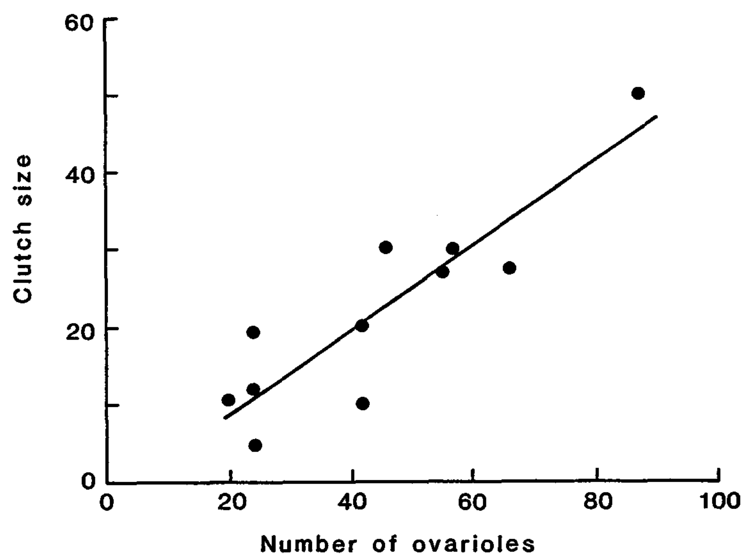

Fig. 1. Mean clutch size in relation to the median number of ovarioles for 11 species of coccinellids.

number of eggs per clutch is approximately equal to half the ovariole number (eqn. 1), which indicates that on average only half the ovarioles are active in the production of a clutch. In insects like coccinellids, in which several eggs develop simultaneously in each ovariole, staggering of production between ovarioles possibly allows a more continuous production of clutches.

TABLE 2

Correlation between clutch size and egg size for 4 species of coccinellid

Species	Correlation coefficient	Range in clutch size	n	Sig
Adalia bipunctata	0.08	6-30	13	n.s.
Propylea 14-punctata	0.32	3-11	11	n.s.
Adalia 10-punctata	− 0.30	4-17	13	n.s.
Coccinella trifasciata	− 0.30	4-20	38	n.s.

Although the first clutches produced by a coccinellid tend to consist of fewer and less commonly slightly smaller eggs than normal, egg size did not vary with clutch size in the 4 species studied. This suggests that the selective pressure(s) acting on egg size is strong and when the reproductive rate is not maximum it is clutch size rather than egg size that is reduced. Therefore at least under standard conditions, egg size can be regarded as fixed. This supports the assumption made in previous work on optimal egg size that there is an optimal size for each given set of environmental conditions (**Williams,** 1966 ; **Gadgil & Solbrig,** 1972 ; **Sibly & Calow,** 1983, 1985). The factors that determine the optimal egg size for each species remain to be resolved, although it has been suggested that non sib competition should result in larger eggs (**Parker & Begon,** 1986). For coccinellids it is likely that egg size is constrained by the foraging efficiency of first instar larvae (they must hatch large enough to catch prey) and by the length of time required to complete development (small eggs take a long time to develop into large adults). These relationships are discussed in detail elsewhere (**Stewart, Hemptinne & Dixon,** 1991).

Thus in coccinellids the allocation of reproductive resources largely depends upon the body design of the species. The number of ovarioles places an anatomical constraint on the maximum clutch size and the number of eggs produced for any given reproductive effort. There must of course be a trade-off in the allocation during development of resources between gonads and soma. An upper limit on gonadal size is imposed by the adult body size and the ratio between the two must be such that an efficient reproductive output can be maintained. The partitioning of gonadal tissue between many large or fewer small ovarioles is therefore a possible mechanism through which selection can act on egg size/clutch size relationships.

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RÉSUMÉ

Volume de la ponte et taille des œufs chez les coccinelles

Il y avait une corrélation positive significative entre le nombre d'ovarioles et le volume de la ponte chez les 8 espèces de coccinelles étudiées. Il n'y avait pas de corrélation intraspécifique entre la taille de l'œuf et le volume de la ponte sous les conditions standard.

MOTS CLÉS : Coccinellides, taille de l'œuf, volume de la ponte, nombre d'ovarioles.

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