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How spiders determine clutch size

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Abstract: The relation (in spiders) between food ingestion during the ripening period of the eggs ans size of the brood show that there is reabsorption of eggs and that the average coeficients of variation for all eggs sizes is closely related to the available sources. These coefficients are higher than those observed for deficient diets ($P < 0.05$). However at time of laying the average size of the eggs is the same. The spiders probably respond to the presence of great quantities of food by iniciating the development of a large number of eggs. If food consumtion is mantained, a series of additional eggs will be produced. Apparently, the physiological processes are linked in a simple manner to the action of a switch. The presence of a certain quantity of food in a given time is the signal that turns on the switch with the incorporation of material into the eggs.

In terrestrial communities spiders are important carnivores in terms of biomass, energy flow and number of species (Van Hook 1971). Studies in diverse enviroments have demostrated that sometimes spiders suffer from starvation under natural conditions (Anderson, 1974; Miyashita 1968). Turnbull (1962) and Miyashita (1968) showed that spiders can survive and reproduce under poor nutritional conditions. Thus, the significance of survival under conditions of starvation is an important aspect in studies of population dynamics and the evolution of spiders (Tanaka and Ito 1968). The relation between food consumption and egg production in spiders was studied in part by Turnbull (1962). This investigation attempts to look further into the dynamics of reproduction in spiders. Several experiments were designed to study the relation between food ingestion during the ripening period of the eggs and size of the brood.

MATERIAL AND METHODS

Acharanea sp. (Theridiidae) generally builds its tangled web in dark places, under stones and fallen logs and between the roots of trees. Mature female of spiders were used for all the observations, collected in a 75 year old forest at Barro Colorado Island, Panama, from December through February 1983, at the beginning of the dry season. Voucher specimens are deposited in the collection of the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica.

Nutritional state of natural populations: Measurements of the body suggested by Anderson (1974) were used as indices of the general nutritional state in the field: weight, width of the cephalothorax, and with and length of the abdomen. An ocular micrometer adapted to a stereomicroscope was used. Fifty individuals were collected weekly and body size, weight, and number and size of the eggs from each female were removed and both length and width were measured.

Experimental animals: Mature young females that were raised to maturity in the laboratory from penultimate instars collected in the field were used for the feeding tests.

Each spider was maintained in a petri dish with sufficient water and food (lab. bred *Dro-*

sophila sp.) at room temperature (27 C), with cycles of approximately 12 hours of light and darkness.

Experiments: When the spiders moulted to maturity, they were acclimatized to laboratory conditions for three weeks, and then divided into six experimental groups: 1 prey every 9 days; 1 prey every 7 days; 3 prey every 7 days; saturation of food (10 prey per day) and without food. Each week a sample of 10 individuals from each treatment were sacrificed (n = 50 for each treatment). Females that had oviposited, were excluded from the treatments.

Food consumption was estimated in terms of live weight. This species does not mutilate its prey and the majority of the corpses can be recovered intact. The bodies that have been consumed can be recognized by treir translucent appearance. The corpses were weighed after each feeding. A second group of flies (n = 200) was killed and weighed; from these the estimated weight of the flies in the population was obtained.

From the difference between both estimates (fly weightaverage corpse weight) the average prey-weight consumed by the spiders in each treatment was obtained.

For the statistical treatment, the methods of U-Mann-Whitney test, chi square, regression and t-student were applied ($P < 0.05$).

RESULTS

Average weight of the natural populations aproximates a mean weight of 0.6 *Drosophila* per day (table 1). Data from the width of the abdomen at different diets and those obtained from natural populations further support this interpretation. One of the most important and interesting adaptations exibited by spiders is reflected in the satiation groups; there is a great abdomen distension which allows spiders to consume and obtain large quantities of food.

The average of the measurements of the cephalothorax do not present significant differences between field and experimental populations (t–student, $P > 0.05$).

There is a direct relation between the rate of weight increment and of food (r = 0.68). In situations of food shortage, the spider utilizes its own tissues to maintain itself (Fig. 2). In all treatments the rates of adult survival were 70-80 % after 60 days. Tanaka and Ito (1968) found that the notable tolerance of food scarcity in *Pardosa estrigers* (Lycosidae) can be attributed primarily to a marked reduction in metabolism. Based on these studies and taking into account the starvation tolerance observed in *Acharanea* sp., this species may also have low metabolic rates. Anderson (1974) demostrated, however, that some Theridiidae have metabolic rates that are particulary high for spiders.

The experimental females (except those without food) were given enough food for egg production in the adult stage, and the numbers or eggs in the abdomens shows a clear relation

TABLE 1

Body weights and sizes of spiders at various levels of nutrition

	Sample size	Abdomen width mm	Cephalotorax length mm	Body weight mgs
Starvation group	250			
Initial		1.28	1.03	.176
Final		1.06	1.02	.104
Station group	50			
Initial		1.19	1.04	.163
Final		1.45	1.03	.342
Field population	600	1.26	1.03	.177

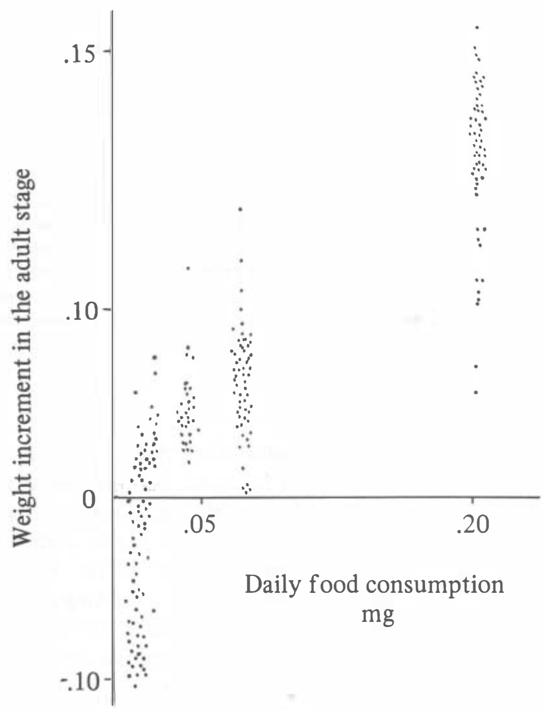

Fig. 1. Daily increment of weight in *Achaearanea* sp. on different diets. A direct relation between rate of increment and food administered is observed.

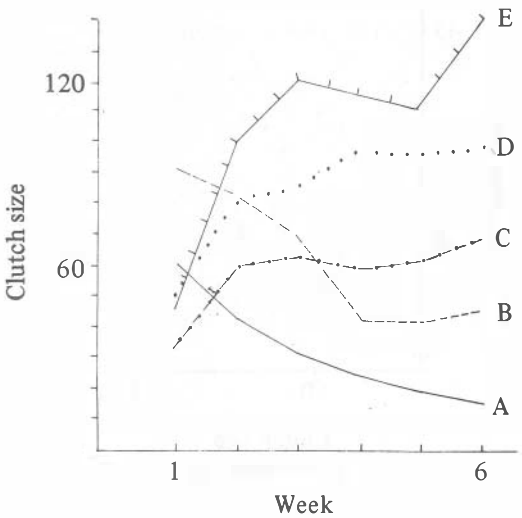

Fig. 2. Relation between the number of eggs in the abdomen and the diet administered. In the diets in which foord was administered frequently and in large quantities (D, E) the average number of eggs increased while the reserve occured in the treatments with deficient diets (A, B).

to the diet administered (Fig. 3). In the diets in which food was supplied frequently and in large quantities (D,E), the average number of eggs increases with time ($P > 0.01$), and the reverse occurs in the treatments with deficient diets (A,B).

Sizes of abdominal eggs were obtained in four other species of different families, collected in the Central Valley in Costa Rica (Figs. 4,5,6,7). If the total number of eggs in the abdomen are divided into two groups in each species (taking as a criterion their average size), and the coefficients of variation of numbers of larger and smaller eggs are compared, there is a significant difference in all species ($P < 0.05$), with lower coeficients for eggs near laying time (larger eggs).

The average coefficients of variation for all sizes of *Acharanea* sp. in the different treatments (Table 1), show that as the food quantity increases, the coefficients of variation are higher than those observed for deficient diets (U-Mann-Whitney $P < 0.05$).

DISCUSION

Eberhard (1979) found an apparent relation between the weight of the spider body and the rate of prey capture. Conservative calculations based on the data of the weights obtained in the field suggested that *Acharanea* sp. averages a capture equivalent to 32% of its body weight daily. This is in agreement with Eberhard's data for orb weaving spiders. The relation between the number of eggs in the abdomen and the diet administered suggest that egg reabsorption occurs under conditions of food shortage. In contrast, in conditions of abundant supply, eggs are added to the developing clutch.

The low number of eggs produced and the low coefficients of variation indicate that the females absorb the eggs when starved.

The average coefficient of variation for all the treatments at the end of the egg development did not show significant differences ($P > 0.05$). The females of this species, like other spiders, adjust their reproduction in the numb er rather than size of eggs (Kessler 1970; Eberhard 1979).

The spiders probably respond to the presence of great quantities of food by initiating the development of a larger number of eggs. If the food consumption is mantained, a series of additional eggs will be produced and since these additional eggs require time to reach the developmental stage of the others, the eggs in these spiders will show a wide range of variation. However, near the laying time no new eggs will be added, and their average size will be more similar.

Recent studies have shown that borod size in spiders depends on several factors; the density of spiders (Wise 1975), size of individuals (Bristowe 1939; Peterson 1950; Eberhard, 1979), nutritional conditions (Kessler 1970), and the age of female (Valerio 1976). Little, however, is known of the physiological and hormonal controls responsible for the development and determination of the number of eggs in each brood. It is inferred from this study that the physiological processes are linked in a simple manner to the action of a switch for the incorporation of material into the eggs, but late in the egg development cycle this switch can no longer be tripped.

Once the first prey is consumed, the future reproductive behaviour will depend basically on the quantity and quality of prey per unit of time that the female succeeds in catching.

Various combined effects are reflected in a greater or lesser degree in each brood produced and it is thus difficult to obtain an integrated

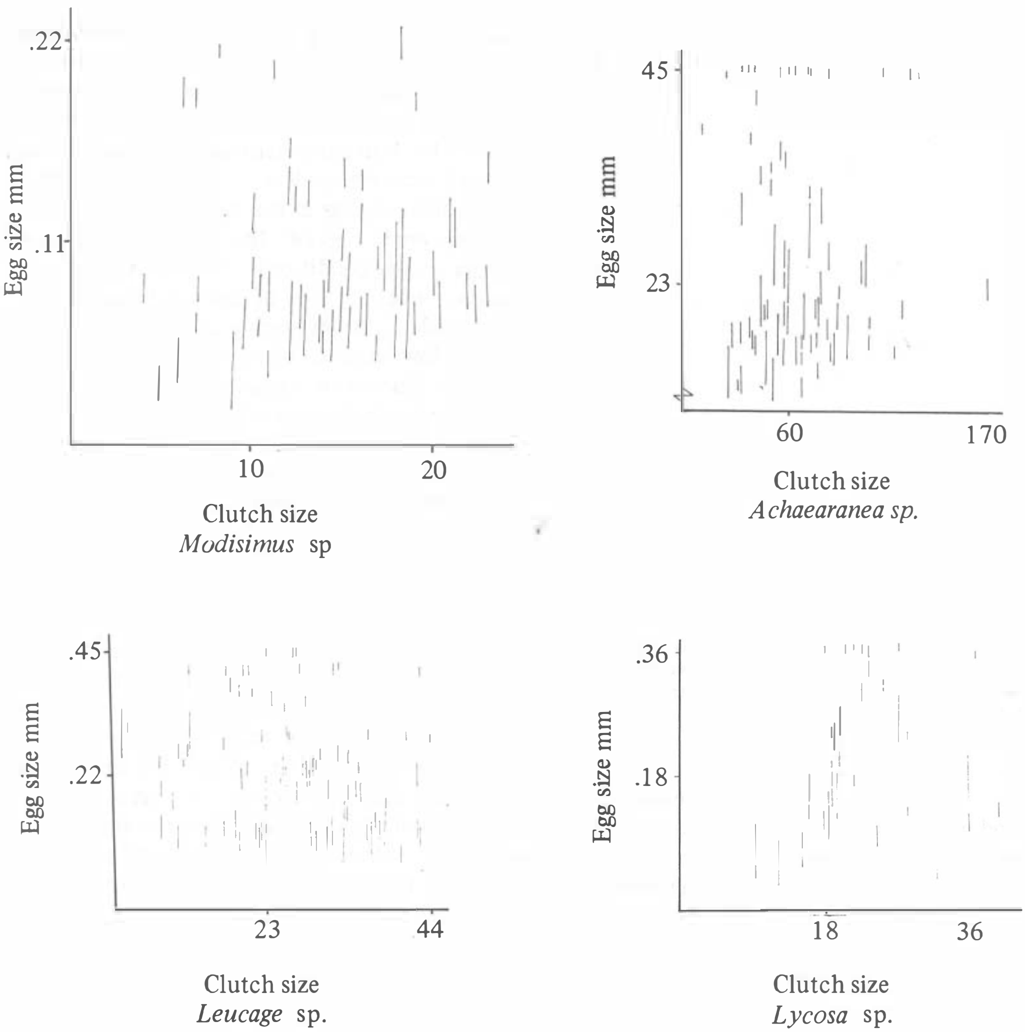

Fig. 3, 4, 5, 6. Numbers of abdominal eggs for natural populations of various species of spiders. Each line represents the range of coefficients of variation for a single spider. If the data are divided into two groups (egg size above or below total average) and the coefficients of variation are compared, broods with eggs near laying time have significantly lower coefficients.

vision of reproduction on spiders and arthropods in general. Nevertheless, the several common patterns shown in this article allow the formulation of the following reproductive strategies that have permitted the spiders to be one of the most successful groups of predators and adapt to a great diversity of enviroments.

1– Flexibility in reproduction, represented by the phenomena of addition and reabsorption of material that permits them to adapt the number of eggs to different conditions of abundant of prey.

2– High reproductive potential resulting from the high capacity of distention of the abdomen, that allows individuals to take **advantage** of large amounts of food.

3– Low metabolic rates in general and a marked capacity to decrease the respiration rate in situations of extreme food shortage with the resulting prolongation in longevity that permits the adults to survive and reproduce during the following cycle.

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RESUMEN

Varios experimentos examinan la relación (en varias especies de arañas) entre la ingestión de alimento durante la maduración de los huevos y el tamaño de la camada. Hay evidencia de reabsorción de los huevos. El promedio de los coeficientes de variación para todos los tamaños de los huevos en los diferentes tratamientos muestra que cuando la cantidad de alimento se incrementa, estos coeficientes son mayores que en los casos de dietas deficientes ($P < 0.05$). Sin embargo, en ambos casos el tamaño de los huevos es el mismo. Las arañas probablemente responden a la presencia de grandes cantidades de alimento iniciando el desarrollo de muchos huevos. Si se mantiene el consumo de alimento, podría producirse un cierto número de huevos. Se infiere que los procesos fisiológicos estan ligados de manera sencilla a una conmutación (switch). La presencia de cierta cantidad de alimento en un tiempo determinado es la señal que inicia la conmutación con la incorporación de material a los huevos.

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