Spider growth as an indicator of habitat quality*

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Summary

A method is presented that allows the calculation of the reserves and thus the food intake of spiders in the field, and the estimation of their daily feeding rate. A laboratory study provides the relationship between the accumulated reserves and growth of Nephila clavipes (L.). Both parameters of growth, the rate (interval between successive moults) and the ratio (size increment during ecdysis), can be observed in the field, and the reserves can be inferred using the calibration curve. The growth ratio can also be calculated from a single sample of the size distribution of a population.

Introduction

Spiders, like other arachnids, are hemimetabolous (ametabolous, paurometabolous). First instar spiderlings leaving the eggsac resemble the adults in most features (Foelix, 1982). Spiders grow in discrete steps but mature without any distinct metamorphosis. In each instar the reserves are accumulated gradually in the abdomen, to be transformed into size increments only during ecdysis (Homann, 1949; Vollrath, 1987). Thus the spider's weight increases gradually with each meal, yet its size changes only occasionally in a sequence of distinct steps. Throughout the spider's life no major changes occur in its habits, with the possible exception of the male's final moult which in many species heralds the beginning of a vagrant, webless, and generally preyless life.

The number of moults from eggsac to maturity may or may not be predetermined (Vollrath, 1987). In most spiders, however, neither the time interval between moults (the growth rate) nor the size increment during a moult (the growth ratio) seem fixed (Bonnet, 1930; Browning, 1941; Jones, 1941; Deevey, 1949; Schaefer, 1976; Miyashita, 1968). Growth rate and growth ratio are usually determined by the feeding schedule, if other influential parameters affecting growth (i.e. temperature, humidity and photoperiod) do not vary excessively (Browning, 1941; Jones, 1941; Schaefer, 1976). The strong correlation between diet, time and growth allows the deduction of a spider's food intake from either its growth rate or its growth ratio, once calibration curves linking these variables to growth have been established. Applying this method in the field makes it possible to determine the food intake of individual spiders (or populations) in different habitats. The method also allows the calculation of the daily food intake of individual spiders in the field.

Methods

In Panama, Central America, the average daily temperature, humidity and photoperiod is relatively uniform within either of the two seasons. During the dry season months of January and February 1981 I raised from one eggsac 60 Nephila clavipes (L.) in the laboratory under average ambient temperature, humidity and photoperiod ($27 \pm 2°$ C, 70% rH, LD 12:12) (see Vollrath, 1983). The spiders were divided into two groups, one was fed Drosophila ad libitum, the other very poorly (1-2 live fruit flies every 4 days). At each moult all spiders were anaesthetised, and then measured and weighed. The measurements were taken on the length of the patella + tibia of leg I, under a dissection microscope fitted with a graticule; the weights were taken with an analytical balance (accuracy 0.01 mg).

In two sites in the field (forest edge and forest) at Cerro Galera I marked spiders individually and visited them daily. During these censuses I recorded the intermoult intervals, collected the exuviae and counted the spiders which were feeding. The growth increment at each moult was calculated from the measurements of successive exuviae. In the same two field sites a population census was taken on 5 January, and the body size of c. 500 spiders measured, using the length of the patella + tibia of leg I. The two sites, (A) forest edge and (B) forest interior, differed from one another in (i) illumination — (A) dark, (B) light, (ii) vegetation — (A) tall trees and little undergrowth, (B) dense bushes bordering tall grass, (iii) wind and rain — (A) sheltered, (B) exposed, and, most important, (iv) prey abundance — (A) low and evenly distributed, (B) high and patchily distributed. For greater details of general methods, sites and the national history of Nephila see Vollrath (1980, 1983, 1985, 1987, in prep.).

The calculation of nutrient reserves

The amount of reserves accumulated during an instar can be estimated very accurately by subtracting the animal's body weight at the beginning of the instar from its weight immediately after the next moult. However, reserves can also be estimated independently of previous measurements. Spiders store all reserves in the opisthosoma (abdomen) (Homann, 1949; Vollrath, 1987). The mechanism of spider growth is described in detail elsewhere (Homann, 1949; Vollrath, 1987, in prep.) and will only be briefly outlined here. A calibration curve showed that body size (as measured by leg length) is very closely correlated with prosoma (cephalothorax) weight. The opisthosoma swells in size during an instar and shrinks again at the next moult, when most of its contents are transferred into the prosoma and legs in order to allow their growth. After each moult no more growth or weight gain is measurable in the prosoma, the food imbibed being stored in the opisthosoma alone. In addition to reserves the opisthosoma of juveniles also contains the silk glands, the heart and the lungs. After a moult these usually constitute almost its entire bulk. Just before the next moult they comprise only a very small percentage.

To simplify the calculations one can equate the opisthosoma weight with the accumulated reserves. Opisthosoma weight can be derived by subtracting the weight of the prosoma and legs from the total body weight. Prosoma weight is calculated with the help of a size-weight calibration curve. Thus the two simultaneous measurements of body size and body weight allow us to deduce accurately the amount of reserves in an animal with unknown individual history.

Calculation of food intake in the field

To illustrate the method of estimating feeding rate and growth rate in the field based on observations in the laboratory, the growth of Nephila clavipes instars 3
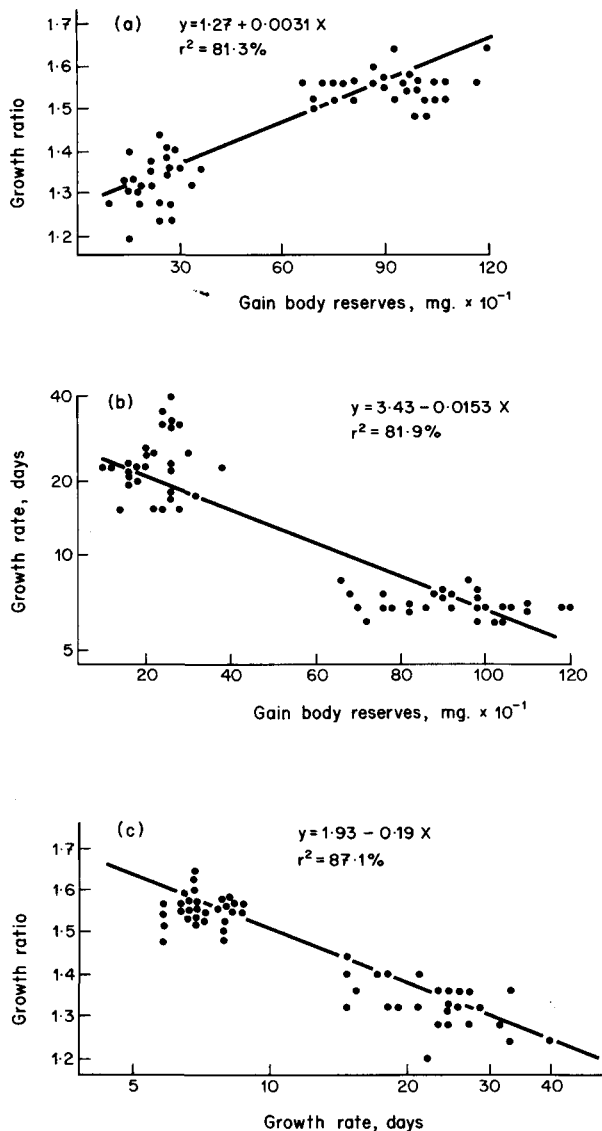

Fig. 1: Growth ratios and growth rate of Nephila clavipes in the laboratory; these graphs represent data taken on one set of spiders moulting into the 3rd (left cluster) and 4th instar (right cluster). **(a)** The size increment during a moult depends on the available reserves. The growth ratio is calculated by dividing the post-moult size by the pre-moult size (in this case length of the patella + tibia of leg I). **(b)** The time interval between successive moults depends on the available reserves. **(c)** The growth rate (interval between moults) and the growth ratio (size increment during ecdysis) are interrelated, the longer the interval the smaller the growth.

and 4 will be examined as an example. The bimodality of the data apparent in Fig. 1 was a result of the two distinct feeding treatments; unpublished observations, made in another context, show that the addition of intermediate feeding regimens will produce an even distribution of points occupying the same space.

Not surprisingly, the growth of animals in the two feeding treatments was significantly different in its ratio as well as in its rate (Fig. 1a, b). A strong correlation exists between the amount of reserves at the time of moulting, and the time span from the preceding moult (Fig. 1c). In the field the growth ratio can be obtained by collecting a moulting individual, and measuring its body size and the size of its exuviae. The growth rate can be measured by observing a marked individual over a period including two moults. From either of these observations the amount of reserves can be calculated (Fig. 2).

From the measurement of the instar distribution of the populations in the field one can estimate the average growth rate in both sites, using the peaks of the distribution as indicators for average instar size (Fig. 2 a — inset). The average growth ratio of these two Nephila populations was 1.35 for the population inside the forest and 1.44 for the population at the forest edge. A number of spiders were followed individually (see also Vollrath, 1985); for these the average growth ratio was ($\bar{x}$ ± s.d.). 1.37 ± 0.08 ($n = 10$) inside the forest, and 1.47 ± 0.07 ($n = 5$) at the forest edge. The intermoult interval inside the forest was 15.2 ± 2.6 days ($n = 16$), and at the forest edge it was 9.4 ± 2.6 days ($n = 12$). The feeding rate (proportion of 100 spiders observed feeding at each site) was 23% inside the forest, and 39% at the forest edge. Thus at the forest edge spiders grew faster (T-test, $p < 0.001$), grew in larger steps ($p < 0.05$) and 70% more were seen to feed.

The data from the field can be transformed into the calibration regression lines fitted to the feeding and growth data collected in the laboratory (Fig. 1a, b, c). This allows us to estimate for each individual spider the reserves accumulated during the duration of an instar. The calculation of the average gain in reserves between moults gave 2.5 mg for the forest habitat and 5.8 mg for the edge habitat, based on the population sample of size frequencies (Fig. 2a). Based on the average growth ratio of the individual observations (Fig. 2b) the gain was calculated to be about 3.2 mg in the forest, and about 6.3 mg for the edge habitat. Basing the calculation on the growth rate gave even higher gain values for both habitats. Since we know the average intermoult interval (15.2 and 9.4 days), we can also calculate the average daily accumulation of reserves. This seems to be about 0.21 mg inside the forest and 0.67 mg at the forest edge, based on the observations of individuals. Individual observations suggested that the feeding rate for spiders at the forest edge was 70% higher than for spiders inside the forest (see above); the now calculated estimate of daily food intake at the forest edge web appears to be 200 to 300% higher than inside the forest. This discrepancy of the two estimates
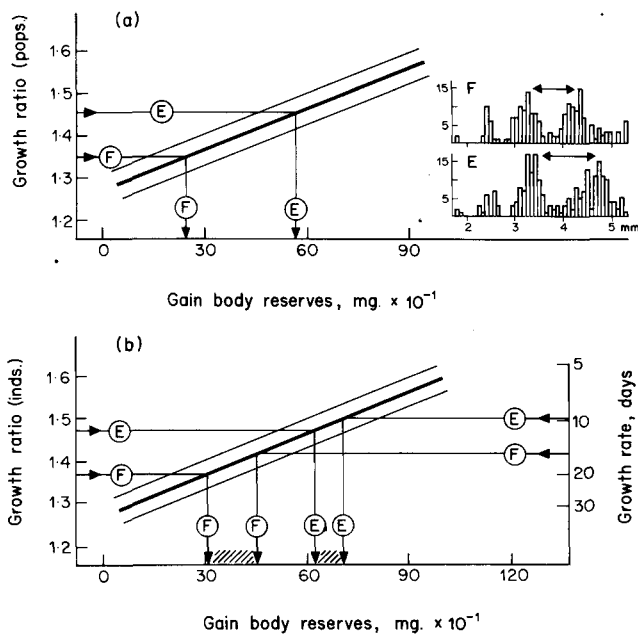
Fig. 2: **(a)** Estimate of the feeding rate based on samples of two populations. The growth ratio can be inferred from samples of a size frequency distribution of two *Nephila* populations inside the forest (F) and at the forest edge (E). A peak corresponds to an instar (abscissa: spider size — length of patella + tibia of leg I in mm, ordinate: frequency). The distance between two peaks represents the average growth ratio. These data are then applied to the calculated relationship between growth rate and feeding rate (regression line of Fig. 1a with standard error). **(b)** Estimate of the feeding rate based on the observations of individual spiders. The amount of reserves accumulated since the last moult can be inferred from either the observed growth rate or the growth ratio. In this particular case a small mismatch exists between the two inferences, which is probably caused by a small temperature effect. However it is clear from both graphs that the forest spiders (F) had accumulated considerably less reserves than the edge habitat spiders (E).

might indicate that the edge habitat provided larger as well as more prey.

Conclusions

It seems from these cross-checks that the method proposed here is rather robust. The method allows, after the construction of calibration curves from a few animals raised in the laboratory, the calculation of the average daily food accumulation and intermoult interval in the field, using a set of calibration curves. Growth rate, growth ratio and feeding rate constitute some of the most valuable information for an understanding of an animal's life history. With this method we have obtained a tool to study these parameters in the field without disruption of the

animals (see also Toft, 1983; Jocqué, 1981). Tedious and laborious observation of marked individuals can be restricted to a few individuals for purposes of checking the method. It must be stressed that in the temperate zones several calibration curves should be calculated for different temperatures. Interpolation, and matching to the average ambient temperature should then allow relatively accurate estimates of the rates and ratios of growth, and of the feeding rates under field conditions.

Acknowledgements

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