Inviable egg production in *Theridion rufipes* (Araneae, Theridiidae): a harvest for first instar spiderlings

Thesis submitted by

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"Some of the spiderlings appeared to feed on the infertile eggs in their egg mass...Further study might show that...this early nutrient (is) of value in survival patterns of a population."

Peck and Whitcomb 1970

"It would be interesting to investigate the hypothesis that sterile eggs in fertile egg sacs have been selected for as 'trophic eggs'."

Jackson 1978

Frontispiece: Prefed and prefasted first instar *Theridion rufipes* spiderlings. There are two such contrasted pairs in this photograph. x 20

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DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

M F Downes

September 1985

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My family, for putting up with it

ABSTRACT

Most of the variability in fecundity and fertility in Theridion rufipes is due to differences between individual females. Food availability is the most influential extrinsic factor controlling fecundity and fertility, and the type of food consumed may also have an effect. Fecundity increases in the later egg sacs of the egg sac sequence.

Neither variations in fixed laboratory temperatures nor variations in prevailing field temperatures affect fecundity or fertility, but both development rate and oviposition intervals are markedly influenced by temperature. At a constant temperature of 20° C, development is halted and oviposition interval is greatly extended. At 25° C and 30° C, development proceeds normally and there is no significant difference in mean oviposition interval.

Some differences exist between the two relatively isolated subpopulations of T rufipes from which experimental specimens were obtained.

The eggs vary in diameter from 0.55 mm to 0.80 mm, the smaller eggs being less likely to develop. The undeveloped eggs are used as a food resource by the first instar spiderlings before they leave the egg sac and disperse. This extra nourishment enables spiderlings to survive without feeding again for up to four times as long as they can without such benefit, enhancing their survival

prospects during the dispersal and habitat-selection phase. Many spiderlings that feed on eggs prior to emergence are able to molt to second instar without further nourishment; the size increase resulting from the molt may widen the available prey spectrum.

The mean proportion of inviable eggs in an egg sac is 0.21 (s.e. = 0.01). These values indicate a marked tendency to provide an amount of extra food-egg yolk material that would approximately double the starvation resistance time during the dispersal and settlement phase. It may be impossible or less efficient to provide an appropriate equivalent amount of extra yolk in each egg at oviposition.

Egg-feeding does not occur in the postembryo stage. An account is given of postembryonic development and a proposal is made for standardization of the terms describing araneid early development stages.

Chapter 1. GENERAL INTRODUCTION

Within the arthropods a broad distiction can be made between those species (in particular among the holometabolous insects) in which feeding is the dominant activity of their larval forms, and those species (primarily among crustacea and most arachnids) in which dispersal and habitat selection is the critical role that the 'larvae' must fulfill.

Spiders fall into the second of the above two categories, their young typically dispersing on the wind in large numbers and making their stake in the Malthusian lottery for a start in life. It is reasonable to suppose that, this stage of the life cycle being the one with the highest mortality, any innovation that confers an advantage upon those undergoing dispersal will be strongly selected.

One such innovation in the reproductive tactics of many spider species may be the provision of extra nourishment to the spiderlings prior to dispersal. This nourishment buys strength, energy, time and sometimes greater size; it comes (not without trade-off costs) in the form of eggs that do not develop but serve as parcels of yolky sustenance that are harvested by the normally-developed young before they set out on their risky journey. This phenomenon also occurs in animals as widely separated phylogenetically as ants (Voss 1981) and sharks (McFarland et al. 1979).

The consumption by spiderlings of such undeveloped eggs was first reported by Becker (1882-96) for the gnaphosid Drassodes lapidosus and by Wagner (1888) for a wolf spider. Lecaillon (1904) observed it among broods of two species of the clubionid Chiracanthium, and since then more than twenty spider species from at least seven families have been the subjects of similar reports. Among the Theridiidae these have included species of the genera Latrodectus (Kaston 1970) and Achaearanea (Valerio 1974).

Holm (1940) had taken cephalothoracic and abdominal measurements of Drassodes lapidosus spiderlings that had and had not fed on undeveloped eggs, and Schick (1972) made similar measurements on a thomisid of the genus Misumenops. Schick also gave results of starvation experiments on 'prefed' and 'prefasted' spiderlings and the effects of drinking water intake on their longevity, finding that egg-feeding increased starvation resistance by 15-62% and that water intake increased starvation resistance time both in spiderlings that had fed on eggs and in those that had not. He was thus the first to demonstrate the quantitative effects, other than body size increase, of inviable egg consumption.

Valerio (1974) drew similar conclusions, in terms of extended early resistance to starvation and potential to molt to a larger size without prior prey capture, from his study of egg-feeding in Achaearanea tepidariorum. However, he used individuals derived from only two egg sacs, so leaving the results in need of confirmatory extension.

Schick (1972) and Valerio (1974) had also suggested that if early extra nourishment led to the young spiders molting without further food intake, this would expand their prey spectrum by increasing body size. Downes (1985) proposed that oophagy might enable spiderlings to escape from unfavourable habitats by allowing them more time for dispersal.

The primary intention of the present study was to investigate whether the production of inviable eggs by adult female spiders was influenced by some environmental variable(s). Ultimately, the optimum ratio of viable to inviable eggs for any given set of environmental conditions may be explicable in terms of parental inclusive fitness, but that is beyond the scope of this investigation.

Assuming that a viable sperm reserve is available, food quality and quantity were thought likely to be the prime determinants of reproductive effort in general (including fertility) and fecundity in particular. Also, because physiological stresses of various kinds increase the further the temperature departs from optimum, it was believed that fecundity and fertility might alter in response to changing temperature. Accordingly, the study aimed to vary these factors experimentally. A further main intention was to see whether fecundity and/or fertility declined over the iteroparous oviposition sequence. Lastly, the extent of the starvation resistance conferred upon spiderlings through oophagy was to be determined.

From four local theridiid species originally considered as subjects for the present study, Theridion rufipes Lucas 1846 (plates 1a and 1b) was chosen as the most suitable. Selection criteria included size (and hence amount of food required), apparent relative frequency of oviposition, ease of handling and amenability to laboratory conditions. Without extensive trials relative suitability could not be quantified but Achaearanea tepidariorum C.L.Koch is far less abundant in Townsville, A. decorata L.Koch is also comparatively uncommon and likes to construct for itself a protective shelter of small leaves, and Latrodectus hasselti Thorell, the adult females of which are seriously venomous, has a longer egg incubation time. Nonetheless, a limited amount of comparable data was obtained on the fecundity and fertility of these three latter spiders and these are presented in Appendix 2.

T. rufipes is widely distributed, primarily in tropical and subtropical regions but with a range extending into temperate zones; it was first described from specimens collected in Algeria. Its original range may be hard to determine because its close association with man has probably led to extensive transportation. A recent first report (Sugarman 1979) of its occurrence in the Marshall Islands, for instance, may reflect its previous introduction by man. In the United States its range includes Texas and Florida (Levi and Randolph 1975).

Plate 1. Theridion rufipes adults

Male (x9) above

Female (x7) below

It is very common in northern Queensland, at least along the coast between Mackay and Cairns, and its Australian range is no doubt much wider. One of a limited number of spider species that typically achieve great abundance in and around man's dwellings and other constructions, T. rufipes is unusual in being virtually restricted to dwelling interiors; it is relatively rarely found on the outside of habitations or under the typically high-set Queensland house. This may be partly or largely due to interactions with another very common synanthropic theridiid, Achaearanea tepidariorum, which is common outside and under northern Queensland houses but is almost never found within them. The same habitat partitioning between these two species occurs in Costa Rica (Valerio 1976) and very likely elsewhere. T. rufipes is probably adapted for life in protected sites generally rather than in artificial dwellings; one population exists deep in a limestone cave complex some 100 Km from Townsville and far from any human habitation.

Chapter 2. GENERAL MATERIALS AND METHODS

Theridion rufipes specimens were obtained from two locations, the interior of a house in Cranbrook, Townsville, and the campus of James Cook University. Most individuals from the latter location came from the enclosed exit stairwells of the Biological Sciences building. The following two methods were used to obtain adult females of known reproductive history:

1. Late instar or penultimate females were located and observed at intervals until they had matured, mated and constructed their first egg sac. They were then collected, and the first egg sac, collected along with them, was considered to be a 'field' sac.

2. Females were collected immature and mated in the laboratory after their maturation molt.

There was thus no uniformity of feeding history, prior to collection, among the specimens used, nor were their ages known. Extensive previous experience with Latrodectus hasselti showed that laboratory rearing was not a better alternative. Reared in captivity, L. hasselti females varied considerably in the number of molts to maturity and in the duration of the stadia (Downes 1986). Food intake could not be uniformly quantified, and the efficiency of web construction and

hence the relative energy expenditure in prey capture was so variable that adult specimens could not justifiably be described as having uniformity of feeding history. Besides, the natural nutritional requirements of L. hasselti (and T. rufipes) is unknown, so the only indication that the conditions of confinement and artificial feeding were suitable for L. hasselti was that most individuals survived to maturity. Since most of the feeding difficulties were more apparent in the early instars, these arguments influenced the decision to use field-collected adults and subadults of T. rufipes in the present study.

Nonetheless, the shortcomings of confinement and diet still apply to the adult spiders collected in the field and used in the laboratory, and these limitations must be borne in mind when drawing conclusions from the results of the investigation.

Confinement in the laboratory was in glass tubes measuring 50 mm x 20 mm with perforated plastic stoppers (plate 2a). Almost invariably the spiders would inhabit the top of the tube, underneath and within the opaque plastic cap; egg sacs (plate 2b) were normally constructed in this location in the tube. T. rufipes will detach her suspended egg sac when disturbed and retreat with it attached to one hind leg. Separating the egg sac from the female without damaging the eggs therefore presents problems, but there is usually a period of at least several seconds between the initial disturbance and the

onset of this protective behaviour. The technique of egg sac removal, then, was to partially lift the tube cap and touch the tarsi of the female's hind legs with a seeker before she 'gathered her wits'. She would drop from the web in the curled-up death-feigning position characteristic of theridiid escape behaviour. Then the egg sac could be transferred untouched, still suspended in the web within the tube cap, by transferring the cap to a fresh tube and providing the original tube with a new cap. Usually within a minute or two the female re-established her normal position in the tube. The unavoidable disturbance of this process may constitute something more than the mere artificiality of confinement considered above. Chapter 10 considers one aspect of disturbance effects.

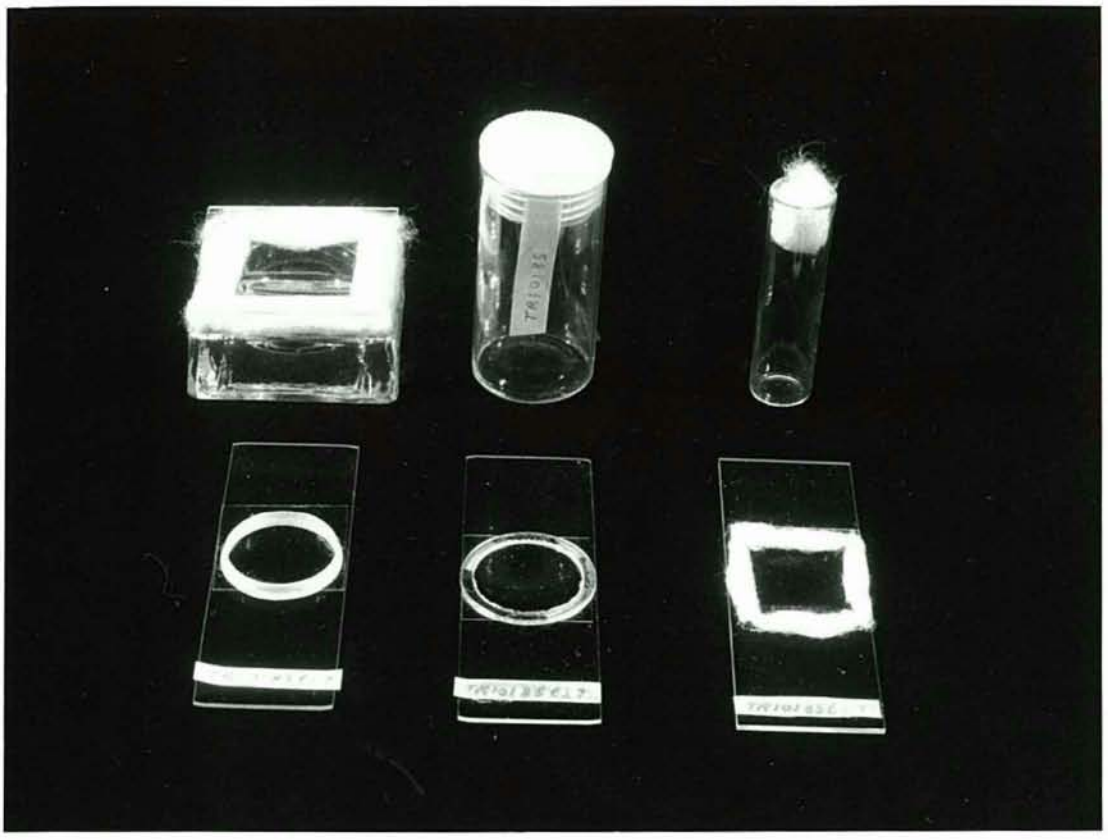
During the times specimens were under experimental investigation in the laboratory they were checked daily. Unfortunately the lifespan of adult female T. rufipes was in excess of the time that could be devoted to their maintenance in this fashion over any single experimental trial. Therefore, the egg sac sequences obtained for the study can only be said to represent total reproductive effort in the cases of those females that died during the course of a given experiment.

Three temperatures, four feeding rates and seven different food types were used in the study. Details of these will be given in the appropriate chapters.

Plate 2.

(a) Containers and slides used in the study

(b) The egg sac of T. rufipes (x8)



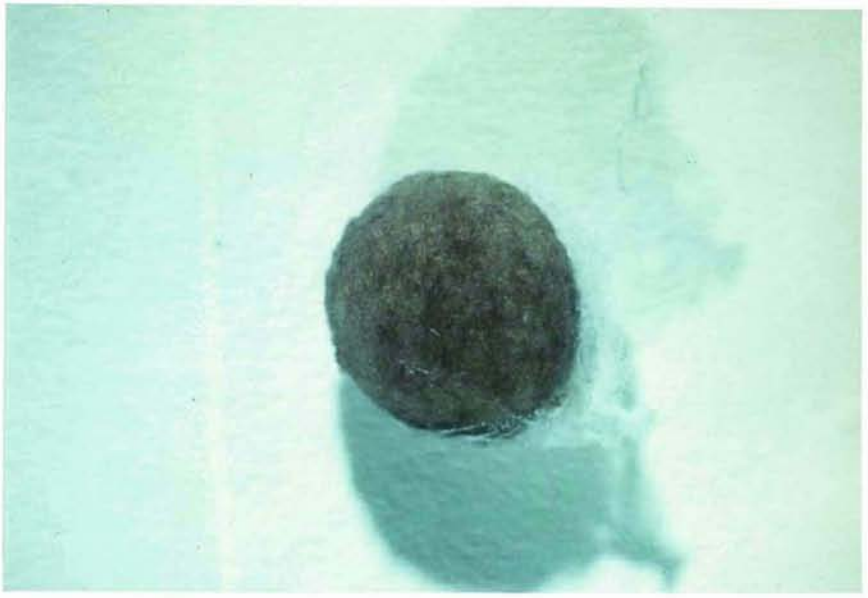
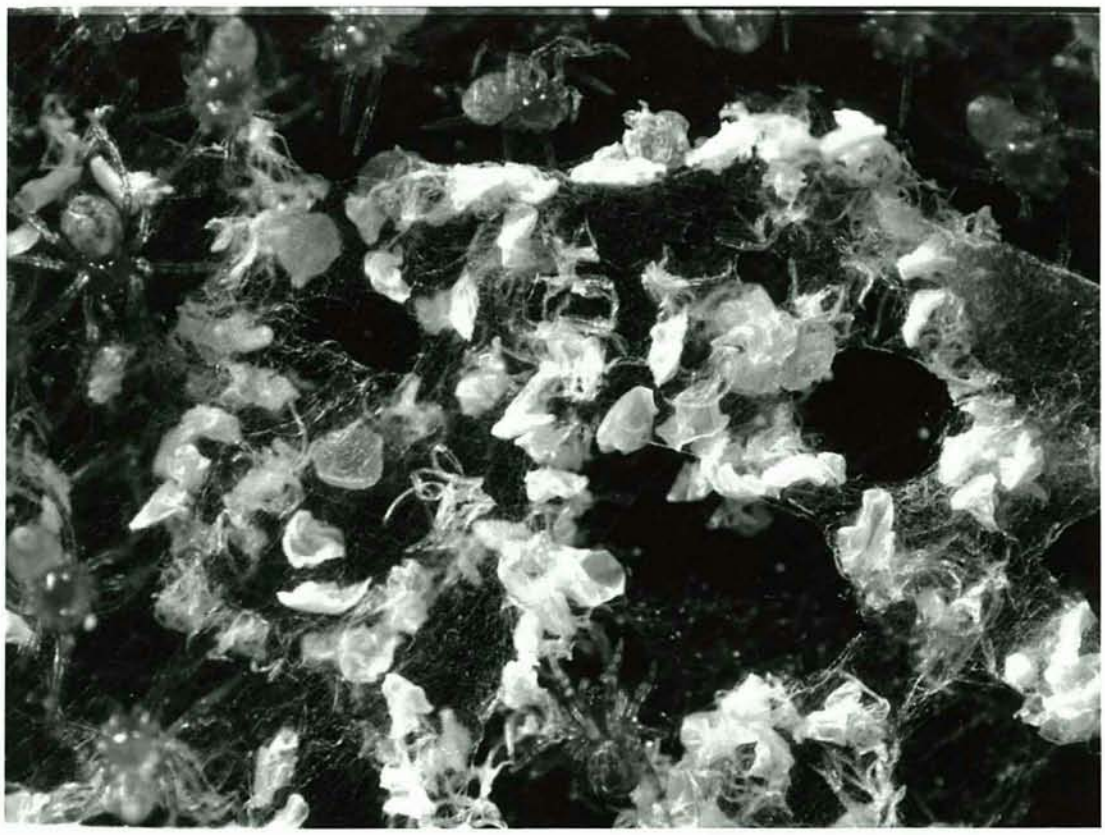


Plate 3.

(a) General appearance of the contents of a full-term T. rufipes egg sac. Visible are empty chorions, half-empty eggs, cast chorions, molt exuviae, a dead postembryo and several first instar spiderlings (x4)

(b) Empty eggshells. Note the crinkled bowl-shaped chorions (remains of feeding)- distinct from the wedge-shaped chorions cast at ecdysis (x30)



Although conceived and largely executed as a laboratory study, it was never forgotten that whatever is happening rightfully happens 'out there'; so egg sacs were collected year round from field locations for comparison with the laboratory results.

The examination of egg sac contents (plates 3a and 3b) after the emergence of the first instar spiderlings was carried out using a stereo microscope. Occasionally sacs contained a few to many eggs congealed together in an obviously inviable mass; in some cases all the eggs were so congealed. This phenomenon has been noted by Bonnet (1935) who ascribed the incidence of such 'conglomerated masses' to the lack of the viscous substance that normally coats the eggs. The 'clumped' eggs of Latrodectus geometricus described by Bouillon (1957a) were probably showing the same deficiency. T. rufipes egg sacs, after the emergence of the first instar spiderlings, typically contained several of the following:

1. First, second (rare) or higher (very rare) instar spiderlings
    (a) living and apparently normal
    (b) living but stuck (e.g. in yolk mass or in malcast exuvium) and/or malformed
    (c) dead
2. Cast exuviae
3. Postembryos, living or dead, with or without attached chorion

4. Cast chorions

5. Unhatched post-reversion embryos

6. Undeveloped eggs

    (a) apparently as laid

    (b) empty (easily distinguished from cast chorions by the latter's characteristic folding)

    (c) partly collapsed

6c above was the source of a problem of interpretation, because the form of partly-collapsed eggs varies considerably. In theory, their condition could have arisen as a result of

(i) degeneration of a fertile or infertile egg that lacked some accessory (e.g. dehydration preventing) factor

(ii) degeneration of a fertile or infertile egg that suffered some puncture or other surface damage that allowed desiccation

(iii) partial feeding by a first instar spiderling (this left a discoloured residue within the chorion; no such discolouration of the chorion occurred when the egg contents were completely consumed)

Since empty undiscoloured chorions only occurred as a result of feeding by a spiderling on a full egg (an already degenerating egg would be at least partly discoloured), and since eggs that remained full and

apparently unchanged at the time of appearance of the first instar spiderlings had shown no sign whatever of development, it was assumed that full and empty eggs were infertile, with the reservation that they might have been fertile but died before any noticeable development. No asssumption of infertility was made (with or without reservation) in the case of partly-collapsed eggs; they were simply considered 'inviable'. One further valid viewpoint, that any individual that did not survive to hatching was also inviable, was taken into consideration. Three assessments of proportional infertility/inviability were therfore made for each egg sac, as follows:

INFERTILITY = (F + MT) / FECUNDITY

INVIABILITY 1 = (F + H + MT) / FECUNDITY

INVIABILITY 2 = (F + H + MT + DPH) / FECUNDITY

where F was full, i.e. unaltered, eggs, H was half, i.e. partly collapsed eggs, MT was empty chorions and DPH was dead pre-hatchlings (not a proposed new term).

INVIABILITY 2 often showed little or no difference from INVIABILITY 1 because so few individuals died as embryos (see Table 3). INVIABILITY 2 is therefore only rarely referred to as a separate formulation of inviability in this thesis.

Records (including the variables for the above formulae) of the contents of each egg sac examined were kept on sac data record sheets (Appendix 1a). Together

with the relevant information for the parent female spider, these records were entered on sac data summary sheets (Appendix 1b) which were used directly as the database for analysis of variance and other computations carried out using the SPSS package implemented on a DEC 10 computer.

The photographs (frontispiece and plates 1-10) were obtained using a Wild M400 zoom photomacroscope.

Throughout the thesis, the 'proportion of developed eggs' in a brood is referred to as the sac fertility, the 'proportion of infertile eggs' as the sac infertility, and the 'proportion of inviable eggs' as the sac inviability. This is done for the sake of brevity. Unless otherwise stated, 'fecundity' refers to the number of eggs oviposited in a single egg sac. It will be necessary to refer also to the total fecundity of particular female spiders; this distinction will be made clear at the appropriate times. 'Inviability' is often used in place of INVIABILITY 1 , where the context precludes misunderstanding.

Methodology specific to particular chapters of this work is detailed in the appropriate sections.

Chapter 3. GENERAL RESULTS AND DISCUSSION (ANALYSIS OF VARIANCE)

Those findings that relate to the investigation as a whole are presented here. This will put the specific results of subsequent chapters into perspective and will minimise the need for repetition and cross-reference.

The study investigated nine potential sources of variation in fecundity and fertility. These were feeding rate (FEEDST), last food type consumed prior to oviposition (FOODTYPE), whether the egg sac was a first, second, etc., sac (SACNO), the origin of the female - Cranbrook or university campus (ORIGIN), the time between feeding and oviposition (FEEDOVIP), temperature (TEMP), the time between a vial change and oviposition (VIALOVIP), whether the female mated in the field or in the laboratory (MATEFORL) and individual variability (FEMALE (= fem. no.)). The name codes for these variables are those used on the sac data summary sheets (Appendix 1b).

MATEFORL was not included in the analysis of variance because inspection showed the results to differ only marginally (see Chapter 10).

Three of the above variables (FEEDOVIP, TEMP and VIALOVIP) showed no significant variations and these will not be considered further here. Of the remainder, only one (FEMALE) is not the subject of a detailed separate account to follow, so the results of the analysis for FEMALE is given here (Table 1). Females produced between one and

twelve egg sacs. For those females kept in constant conditions throughout the observation period, the analysis below compares the average fecundity and fertility of sacs from different females.

Table 1. Fecundity and fertility variation between individual females, with and without respect to feeding rate. One-way analysis of variance. Degrees of freedom (df) given as treatment, residual.

Feed rate		df	F	sig
Subminimal	Fec	8,5	0.166	0.9867
	INVIA 1	8,4	4.519	0.0809
	INFERT	8,4	3.639	0.1138
Minimal	Fec	24,78	1.117	0.3460
	INVIA 1	24,76	17.962	0.0001
	INFERT	24,76	7.703	0.0001
Normal	Fec	13,35	3.934	0.0006
	INVIA 1	13,34	2.031	0.0488
	INFERT	13,34	4.539	0.0002
Maximal	Fec	28,151	2.260	0.0009
	INVIA 1	28,142	7.635	0.0001
	INFERT	28,142	16.842	0.0001
Combined rate	Fec	62,234	3.114	0.0001
	INVIA 1	62,222	7.573	0.0001
	INFERT	62,222	13.504	0.0001

The individual variations between females in Table 1 were computed separately for each feed rate. This was because feed rate was the only other variable whose effects on fecundity and fertility were always highly significant.

The values in Table 1 are one-way ANOVA values (factorial analysis required narrower limits on degrees of freedom). The amount of the total variance explained by these individual differences was 73% (fecundity), 79-82% (inviability) and 74-84% (infertility).

Table 1 shows that individual females of T. rufipes vary markedly in their reproductive performance. That is, when kept in constant feeding conditions, the egg sacs of particular females tend to be very similar. This is not so for fecundity at low and very low rates of feeding; at these feed rates fecundity is much reduced (see Chapter 8) and reproductive effort may be constrained within narrower limits, giving the potential for individual variation less chance of expression.

The degree of individual variability suggests that those results of this study that are based on data from low numbers of individuals must be viewed with some caution.

The effects of the remaining four variables (and their contributions to the total variance) are shown in Table 2.

Table 2. The effects of FEEDST, FOODTYPE, SACNO and ORIGIN on fecundity and fertility. Four-way analysis of variance, using a total of 325 egg sacs.

Variable		df	F	sig	% cont
FEEDST	Fec	3	29.690	0.001	19
	INVIA 1	3	13.541	0.001	10
	INFERT	3	13.407	0.001	10
FOODTYPE	Fec	4	4.349	0.002	4
	INVIA 1	4	6.984	0.001	8
	INFERT	4	0.837	0.480	1
SACNO	Fec	3	4.052	0.008	3
	INVIA 1	3	0.842	0.472	1
	INFERT	3	0.555	0.645	1
ORIGIN	Fec	1	6.386	0.849	0
	INVIA 1	1	7.570	0.063	1
	INFERT	1	21.163	0.001	4

In Table 2, FOODTYPE excluded wasps because the latter was used so rarely; SACNO was condensed into four groups of three consecutive sacs. These measures minimised the workspace for the computation. The more detailed accounts given in the appropriate chapters of this thesis include uncondensed results obtained by one-way analysis of variance.

For the present purpose it should be noted that fecundity in T. rufipes is influenced by three of the four

variables of Table 2. FEEDST and ORIGIN (the latter possibly having some basis in the demic population structure or juvenile history - see Chapter 9) affect the fertility rate, and FEEDST, ORIGIN and FOODTYPE affect proportional inviability. It is clear that the feeding variables have the largest effects.

Interpretations of these results will be discussed in the appropriate chapters. It will suffice at present to have seen which variables are the most important in their effects on fecundity and fertility. These are: individual differences (by far the most significant factor), feeding rate (the most significant extrinsic factor) and three other factors of relatively small importance - food type, sac number and origin.

Chapter 4. POSTEMBRYONIC DEVELOPMENT

Section 4.1. Introduction

This chapter serves two purposes. One is to provide a descriptive account of postembryonic development in Theridion rufipes and the other is to give some quantitative information on the rate at which this development proceeds. These topics taken together constitute the developmental background against which egg-feeding occurs. Similar accounts of postembryonic development have also proved to be of fundamental importance in the elucidation of complex taxonomic problems in a number of spider genera (Seligy 1970).

Unfortunately a Tower of terminological Babel has arisen astride the developmental biology of spiders, making interpretations of events often difficult and sometimes irreconcileable. The attention given in this study to the rate and sequence of developmental events was designed to preclude any doubt about how in T. rufipes the oophagy phenomenon relates to eclosion, ecdysis and emergence. Out of this arose a formulation of a terminological scheme which would, if accepted, standardize future reports and promote compatibility of results.

The major features of late embryonic and early postembryonic development in spiders are reversion

(inversion), hatching (eclosion) and the first true molt (ecdysis). Reversion is an embryonic event unique to arachnids and is a reversal of the orientation of the embryo with respect to the vitelline mass (Dawydoff 1949, Foelix 1982, Savory 1977). It will not be considered further here.

There are three unresolved problems that bedevil the description of events subsequent to reversion. Firstly, there is no agreement on the point at which the embryonic period ends. Secondly, there is no consistent convention in numbering the instars, or rather in defining the features of the first instar. Lastly, as intimated above, a number of inappropriate and misleading terms have been coined to label the various stages of development. As a result of these difficulties it is often hard in any given report to determine whether the 'postembryo' is enclosed in (a) a 'membrane' (b) the embryonic cuticle or (c) the integument. An attempt is made below (subsection 4.4.1) to rationalize these problems. Because subsection 4.4.1 necessarily details the findings of previous authors who have studied this phase of spider development, the same ground will not be covered here.

As in all poikilotherms, temperature is usually the most critical environmental factor influencing the rate of development. However, an animal rarely develops under a constant unchanging temperature regime, but rather experiences daily temperature variation around a gradually changing seasonal mean. Latrodectus hasselti commonly

experiences temperatures of 30° C or greater in Townsville, but 30° C is close to an upper limit of temperature tolerance if applied continuously (Downes 1986). A comparable effect, involving a low rather than a high temperature, was encountered in T. rufipes in this study.

Section 4.2. Materials and Methods

Development rate data were obtained at two of the three temperatures (20, 25,and 30° C) employed to investigate temperature effects on fecundity and fertility. Development did not occur at 20° C. The photoperiod was in each case 14/10 hr light/dark. Development times were recorded in days. Not unexpectedly, there were more records (189) of oviposition - emergence times for undisturbed egg sacs than there were of hatch times (63) and times to first molt (40) using opened egg sacs. Hatching is taken to occur at the time of the first rupture of the chorion.

Intact egg sacs were enclosed in 50 mm x 20 mm glass tubes with perforated plastic stoppers (Plate 2a). Egg sacs opened for observation were housed in glass cavity blocks the glass covers of which were separated from the rims of the blocks by a layer of non-absorbent cotton wool, with a little vaseline as adherent. For photography, microscope slides prepared in a similar way were used (Plate 2a). These were kept in the same locations as the intact incubating egg sacs and were examined at intervals

using a stereo microscope.

When mating was observed, it was possible to record the time from mating to the first oviposition. Times in days between subsequent ovipositions were routinely recorded for all laboratory specimens.

Section 4.3. Results

Subsection 4.3.1. An account of development to first instar

The eggs of T. rufipes (plate 4a) are normally pale off-white or cream-colour (on a few occasions a rich yellow) and are robust enough to resist minor shocks. They will usually develop normally even if dropped through distances of 50 mm onto hard surfaces. They roll freely and do not stick to each other or to supporting surfaces. Occasionally, however, egg masses may become 'congealed' (Chapter 2).

Embryonic develoment was not investigated, but frequent casual observation of developing eggs showed that early differentiation is marked by minor denting and collapse of the egg sphere. A general fine mottling of the chorion (or mottling of underlying structures seen through the chorion), was also observed prior to the appearance of any recognizable anatomical features, and the localization or polarization of germ tissue at one locus of the sphere was characteristic of all viable eggs. These vague

features preceded reversion. Between reversion and eclosion (Plate 4b), the dorsal surface of the embryonic cephalothorax rises above the general surface level of the sphere, and the developing limbs appear, hugging the vitelline mass, their tarsi interlocking at the tips (Plate 6a).

Lines of stress within the chorion, lying at right angles to the future shell rupture line, become apparent prior to hatching (Plate 5a). The first breach of the chorion occurs across the point of the embryonic chelicerae and rapidly traces a split along both sides at about the level of the coxae (Plate 5b). The ruptured chorion is now unevenly divided into a large posteroventral 'bowl' and a smaller, flatter dorsal 'lid', hinged at a point above the position of the pedicel.

The chelicerae and pedipalps emerge first (Plate 6a), and the legs are gradually drawn free as both portions of the chorion slide back, finally to gather as a wedge of tissue which remains attached to the posterior tip of the abdomen (Plate 6b) until it is mechanically dislodged by the motion of the hatchling's closely-packed broodmates or until it is cast free along with the exuvium of the first molt. At no stage was a vitelline membrane observed; if it exists, as it probably does, it must be closely bound to the chorion.

Hatching constitutes the first notably hazardous event in the life cycle of T. rufipes, although it is less risky than the first molt judging by the relative numbers

of individuals that were found dead apparently as a result of unsuccessful hatching or unsuccessful molting (Table 3).

Table 3. Death likelihood and development failure prior to emergence: values are (affected individuals in a sac/sac fecundity) for n sacs.

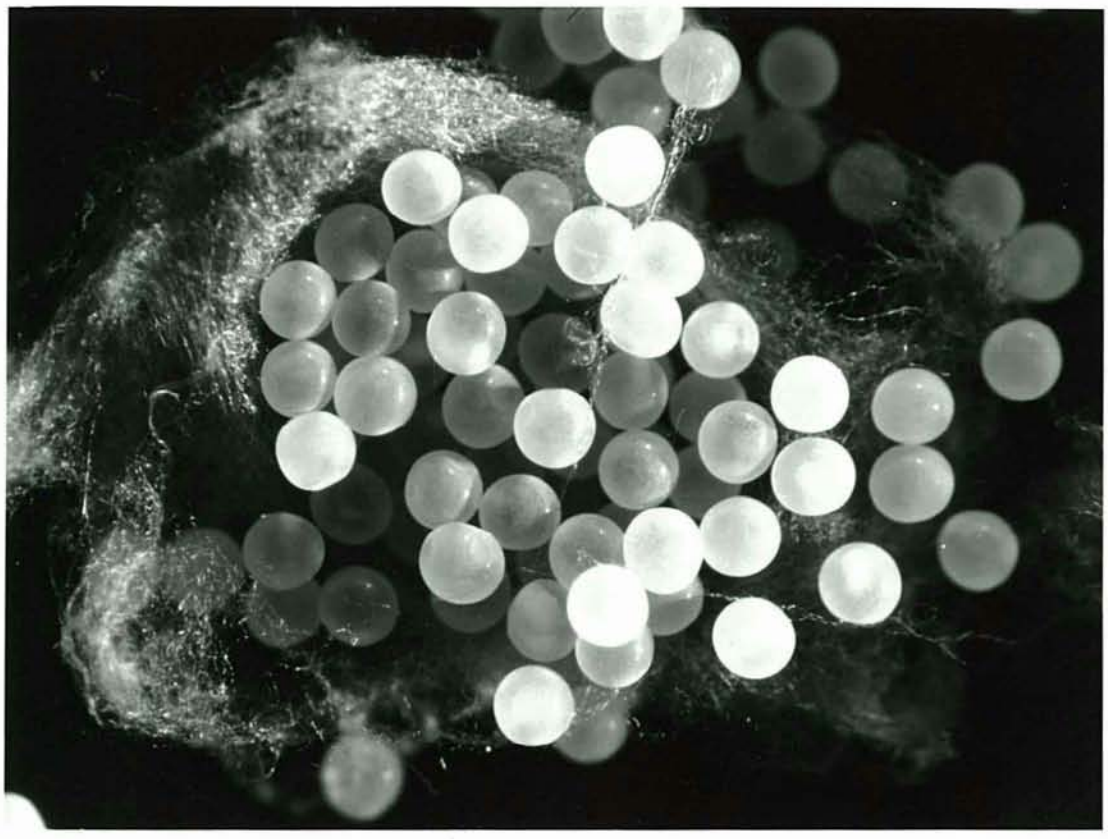
	mean	s.e.	n
Death in first instar	0.037	0.004	763
Death as postebryos	0.007	0.001	763
Death before hatching	0.003	0.001	763
Defective molting or malformation	0.016	0.002	763

The value for death before hatching in Table 3 may be largely due to unsuccessful reversion, but this cannot be proved. The dead postembryos were in many cases seen to be victims of hatching problems; the dead first instars frequently had not completed ecdysis properly. Those first instars which were stuck to exuviae as a result of unsuccessful molting or were malformed for similar reasons, while not dead, can be taken to be victims of this hazard. The relatively high mortality during the first molt may be largely due to the increased activity of the first instar spiderlings within the close confines of the egg sac prior to emergence. This would be substantiated if it could be shown that most first-molt failures occur among late-developing individuals.

Plate 4.

(a)The eggs of T. rufipes. Differentiation of germ bands visible in some of the eggs (x14)

(b) Post-reversion stage. Three of the four central individuals in early phase of this stage. Others are close to hatching (x32)



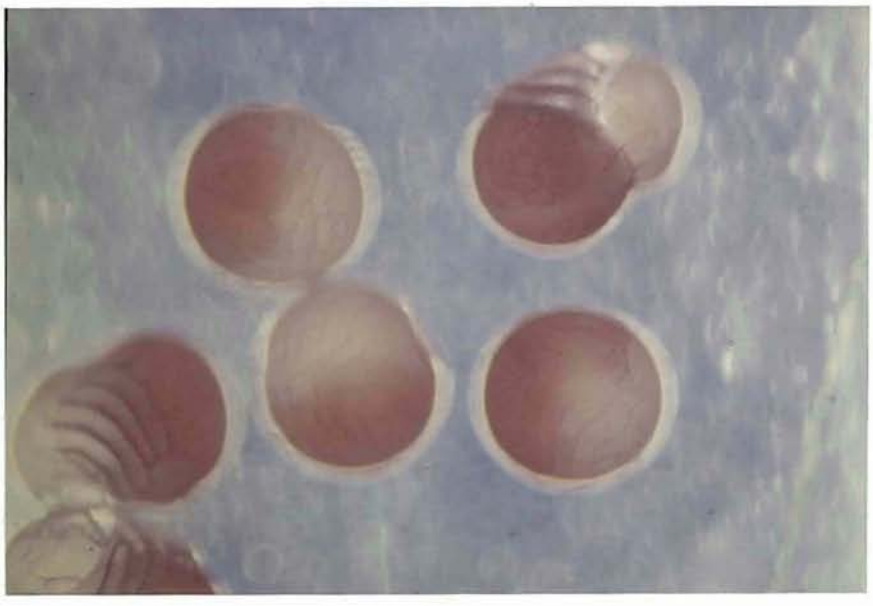


Plate 5.

(a) Hatching - chorionic stress. Note stress lines, especially dorsal from cephalothorax to abdomen (x45)

(b) Hatching - rupture of the chorion (x32)

Plate 6.

(a) Hatching - disposition of the appendages (x32)

(b) Postembryos - general appearance. Note individual as yet unhatched (off-centre) (x20)

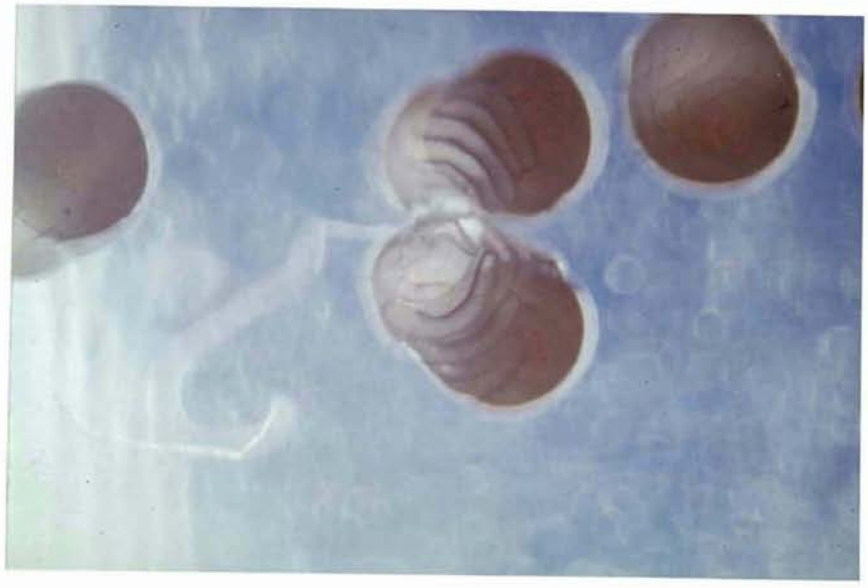


Plate 7.

(a) Postembryo - eyes and pedipalp segmentation (x32)

(b) The first moit - flexure (x15)

Plate 8.

(a) The first molt - extension (x15)

(b) Exuvium of the first molt (x30)

Plate 9.

First instar spiderlings (x20)

The postembryo spiderling (Plate 6b) that emerges from the chorion at eclosion is, apart from its denser, mottled abdomen, pigmented only in the anterior median eyes (in some individuals, some pigment occurs in other eyes (Plate 7a)) and along two small posterolateral cephalothoracic streaks. The cephalothorax and appendages have a translucent, jelly-like appearance. The chelicerae are without fangs and are not free to move. The pedipalps, if not truly segmented, are at least constricted at future segmental junctions (Plate 7a), as are the legs. The labrum is defined. Small hairs, often difficult to see on early hatchlings, are visible but they arise from the cuticle of the first instar stage and they therefore lie flat, depressed and covered by the semi-transparent integument of the postembryo which itself bears no such hairs.

These postembryo spiderlings cannot stand or locomote in any way. The motile ability they do have is largely restricted to a feeble flexing of the legs. This very limited power of movement does not appreciably change until the first molt. Peaslee and Peck (1983) reported the same thing for Octonoba octonarius.

Although the postembryo stage is short, normally lasting a day or two, some developmental advances do occur during this time. The position of the lung books becomes more obvious and the coxae take on a better defined appearance although they are not sharply delineated from the sternum. The non-functional spinnerets may become

slightly better defined from their earlier appearance as four elevated bumps, and a posterior median protuberance is presumably the colulus. Above all, the body hairs become larger and thicker but still lie flat beneath the cuticle (which is to be shed as the first exuvium), making the 'pharate' nature of this stage very obvious, as was the case with Valerio's (1974) observations on A. tepidariorum.

Peck and Whitcomb (1970) have described how the postembryo stage of Chiracanthium inclusum grows actively, doubling its carapace width, and they suggest that this supports the view that the postembryo stage is fundamentally different from the stages following and should not be included in the instar sequence. In addition to such external development, very important organogenesis occurs during the postembryo period (Vachon 1957).

During the first ecdysis (Plates 7b and 8a) the abdomen, held at right angles to the cephalothorax, undergoes considerable elongation, but regains its normally more rounded form after the exuvium (Plate 8b) is shed along with the chorion which all this time has remained attached to the posterior tip of the abdomen. The almost newly-emerged first instar spiderling undertakes a good deal of leg movement to clear the final parts of the exuvium from its tarsi, rather like a wiping of sticky fingers and probably for the same reason. First instar spiderlings were not uncommonly found stuck by a tarsus to a cast exuvium and thus trapped inside an egg sac after

the exodus of their more fortunate siblings.

The body hairs now stand erect on the first instar spiderlings (Plate 9) which are fully motile and spin silk freely, as could O. octonarius first instar spiderlings (Peaslee and Peck 1983). The sternum is clearly marked off from the line of the coxal bases. Claws (including palpal claws) are present, as are fangs on the now freely moving chelicerae. The anterior lateral eyes, and in some cases the posterior eyes, show more pigment. The cephalothorax and legs are still translucent but within a day or two they take on a golden-brown hue that matches the bronze-coloured abdomen.

Subsection 4.3.2. Developmental rates

Mean times from oviposition to eclosion, ecdysis and emergence (i.e. the absolute duration of the embryonic, postembryonic and in-sac first instar spiderling stages) at 25° C and 30° C are given in Fig 1a. This shows that the temperature increase of 5° C from 25° C produces a proportional decrease in development time of 0.28 for the embryonic stage, but of only 0.14 for the postembryonic stage. Despite the fact that the overall development time from oviposition to emergence decreases by a factor of 0.15 with the same temperature change, the within-sac first instar stage time actually increases by a factor of 0.33, i.e. from 2.4 to 3.2 days.

Fig 1a. Mean development times from oviposition to hatching (H), molting (M) and emergenge (E). Standard errors (too small for inclusion in the figure): 25° C - H,0.18; M,0.32; E,0.77. 30° C - H,0.27; M,0.37; E,0.27. Numbers of cases: 25° C - H,48; M,27; E,124. 30° C - H,15; M,13; E,65.

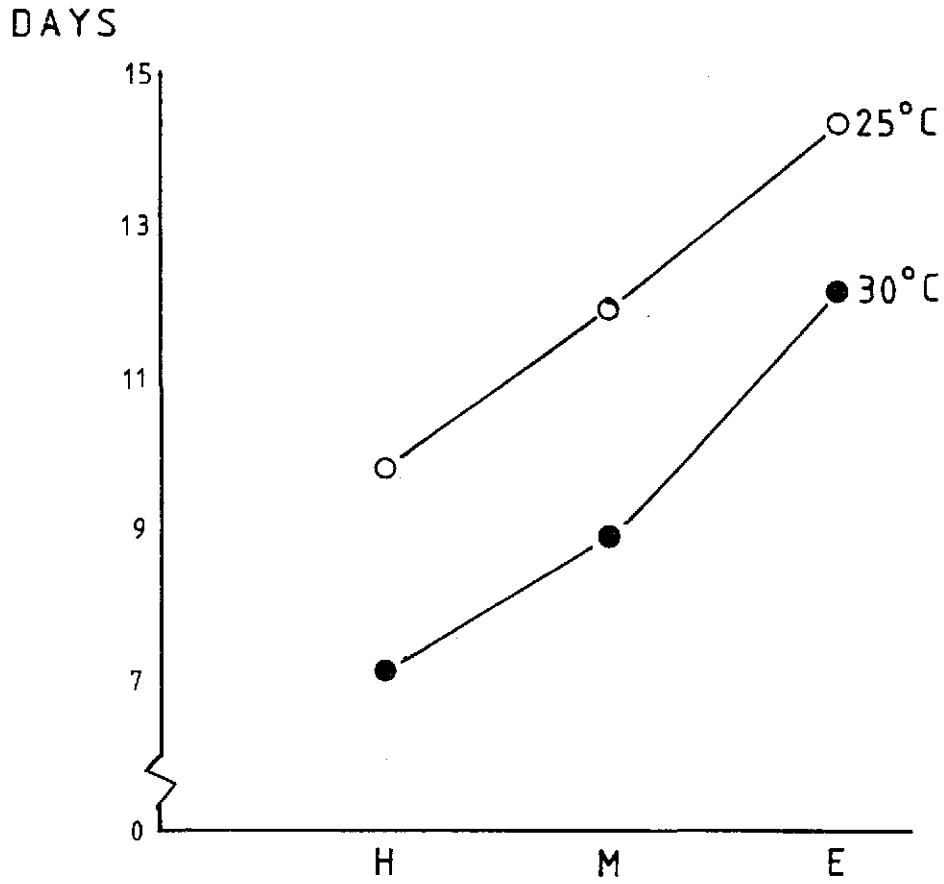
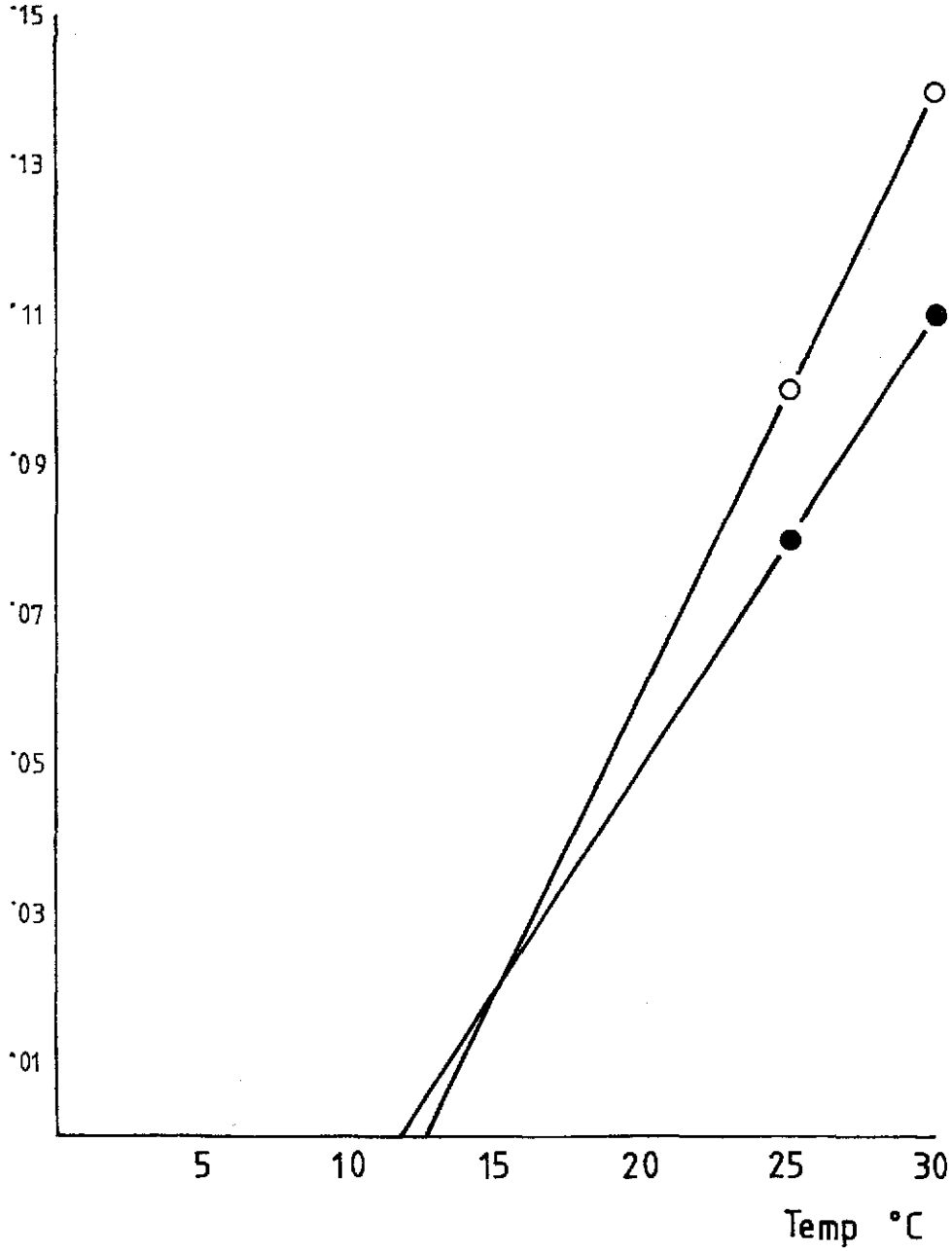

DAYS
15
13
11
9
7
0
25°C
30°C
H
M
E

Fig 1b. Embryonic and postembryonic development rates. Black dots, postembryos. Open dots, embryos.


·15
·13
·11
·09
·07
·05
·03
·01
5
10
15
20
25
30
Temp °C

Development rates with respect to temperature (Fig 1b) are presented using the limited data available. Fig 1b gives a developmental threshold of 12.5° C for the embryonic period and 12° C for the postembryonic period. Using these threshold values for calculation of day-degree values (Wigglesworth 1972) for development, the following values are obtained:

Embryo	122.5 (25° C)	124.2 (30° C)
Postembryo	27.3 (25° C)	32.4 (30° C)

There was no evidence that the adult female spiders were adversely affected by the experimental temperature extremes of 20° C and 30° C. However, the oviposition sequence was significantly extended by reduced temperatures. Times, in days, separating the ovipositions of the iteroparous sequence are presented in Table 4. It is unfortunate that so few (3) cases were available for mating-oviposition at 20° C because the mean of these few values is by far the highest of those presented.

Table 4. Effect of temperature on mean time from mating to first oviposition and between subsequent ovipositions. Values given as mean interval in days, with standard error and (number of cases).

	Mating-Ovip 1	Subsequent Ovips
20° C	47.7, s.e. 0.37 (3)	26.2, s.e. 2.16 (38)
25° C	6.6, s.e. 1.03 (17)	16.1, s.e. 0.57 (123)
30° C	6.3, s.e. 1.08 (11)	14.1, s.e. 0.61 (95)

The time between mating and the first oviposition is in general much shorter than between subsequent ovipositions, but it is more markedly increased by low temperatures.

Table 4 also shows the dramatically suppressive effect of a surprisingly high temperature (20° C), only 5° C below what is probably close to the optimum for T. rufipes development and reproduction. The marked effect of this same temperature reduction on the development of T. rufipes eggs has been noted above, and the developmental threshold of about 12° C coincides closely with the oviposition interval threshold suggested by Table 4. The 5° C rise from 25° C, although decreasing the mean oviposition interval, does not compare in effect to the equivalent drop of 5° C from 25° C.

This, and the developmental data previously discussed, suggests that unlike most insects which have been studied, the relationship between temperature and developmental rate may be markedly non-linear during some life-stages in this species.

Section 4.4. Discussion

Subsection 4.4.1. A review of early postembryonic development in spiders

In common parlance 'hatching' is emergence from an enclosing eggshell; but eggshells consist of more than one

embryonic membrane. A problem arises when attempts are made to define hatching in organisms that do not shed all embryonic membranes simultaneously, and the more membranes involved the more scope there is for confusion (indeed, the present state of the descriptive art in araneology resembles Ptolemy's epicycles). Vachon (1957) may be right in his view that hatching as such is of secondary importance and that no significance should be attached to the point of development at which it occurs, but it is necessary to have a recognized framework of the event sequence so that descriptions of the transitional process from embryo to 'complete' spiderling are comparable and therefore throw light, not confusion, on the systematic, evolutionary and adaptive relationships among the species studied. Certainly it is a most important fact that all spiders do not hatch at the same ontogenetic stage (Holm 1940).

The process of membrane rejection, at least, is similar in most if not all spider species: a membrane ruptures across the base of the chelicerae, perhaps initiated by the secretion of hatching enzymes from pedipalpal glands (Yoshikura 1955) but usually assisted by the egg-teeth (cuticular denticles) which extrude as points from the embryonic cuticle and are shed along with the latter. The membrane then splits along the ventrolateral line of the cephalothorax at about the level of the coxae and recedes posteriorly to the tip of the abdomen. More often than not it remains attached at this

position and is cast with either the shedding of a subsequent membrane or with the exuvium of the first true integument molt. A useful definition of a true molt is one that has limbs (Davies, pers. comm.).

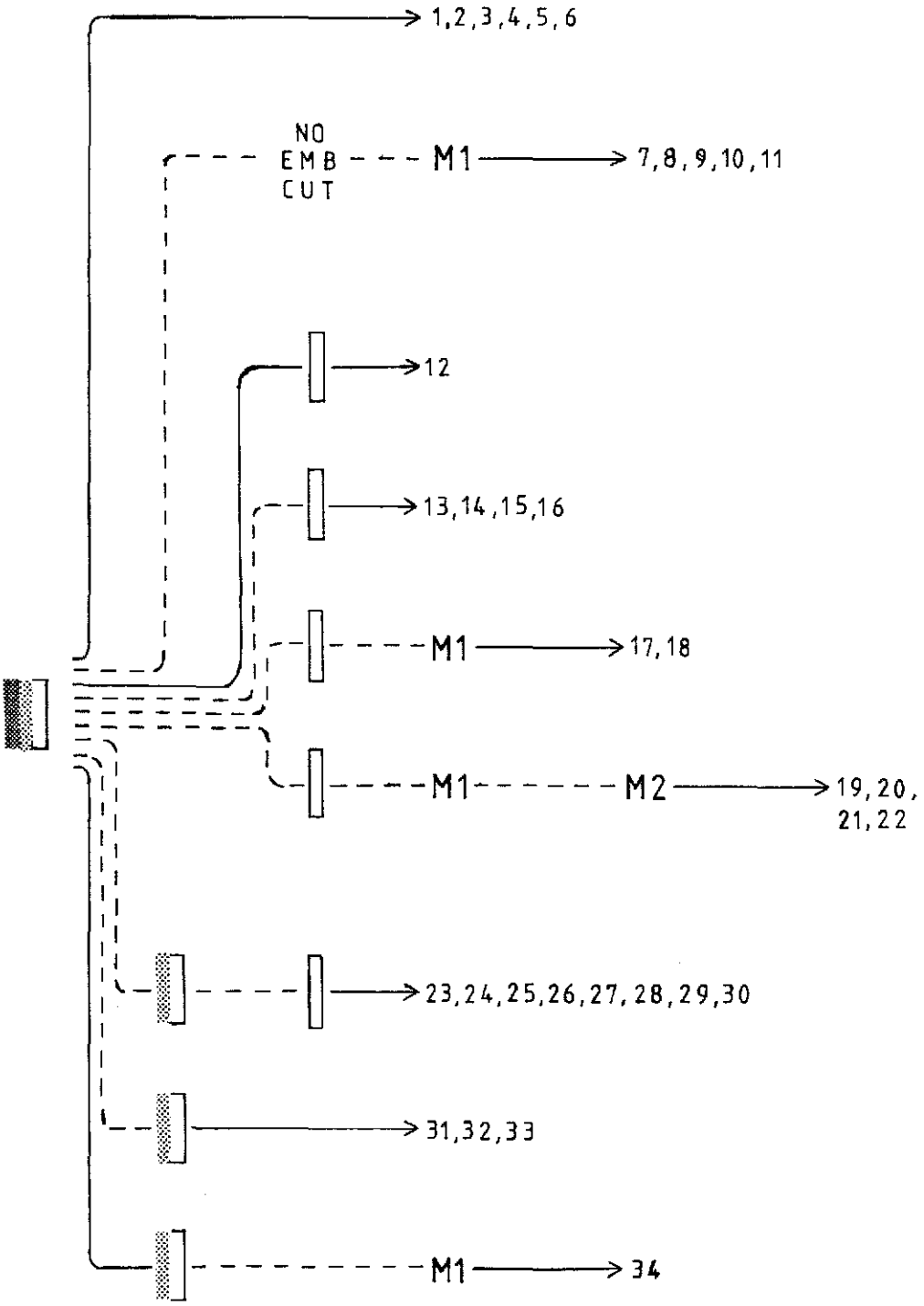
Fig 2 brings together in a comparative schema various authors' descriptions of the embryo-postembryo transition for 27 species or higher taxa of spider. It is unlikely that the schema is without error (of observation by original authors and/or of interpretation by the present one); if there were no irreconcileable confusion between the reports there would be no need of a comparative revision. The absence of the embryonic cuticle, where stated in Fig 2, is based on observations made on T. rufipes and other theridiids in this study and on Holm's (1954) claim that the embryonic cuticle is suppressed in the Argiopiformia. The latter includes the Theridiidae but it is not a useful higher taxon today; nor is the Dionychae (the two-clawed spiders).

In Fig 2 hatching is considered to begin with the rupture of the chorion and end with the discarding of the embryonic cuticle. In several cases the latter is not discarded until the first true molt, and in one case not until the second molt. This 'definition' of hatching has more than an arbitrary usefulness because whereas 'postembryonal' (i.e. 'incomplete') stages may or may not be free of all membranes, no 'complete', active and ambulatory stage ever has attached membranes still undiscarded.

Fig 2. The hatching process in spiders: a schematic presentation of the results of fourteen authors. Dark band, chorion; stippled bands, vitelline membrane; light bands, embryonic cuticle. Dashed lines, shedding without total rejection; continuous lines, shedding with total rejection (including simultaneous rejection of any previously undiscarded membrane(s)). NO EMB CUT= no embryonic cuticle (suppressed in the Argiopiformia (Holm 1954)). M1= first true integument molt; M2= second true integument molt.

Example - species 23-30 shed chorion without casting it completely; subsequently shed vitelline membrane but again without casting it completely; subsequently shed and cast totally the embryonic cuticle along with the still as yet unrejected chorion and vitelline membrane.

Key overleaf


1,2,3,4,5,6
NO
EMB
CUT
M1
7,8,9,10,11
12
13,14,15,16
M1
17,18
M1
M2
19,20,
21,22
23,24,25,26,27,28,29,30
31,32,33
M1
34

Key to Fig 2.

1. *Grammastola pulchripes*	Theraphosidae	Galiano 1969b
2. *Grammastola vachoni*	Theraphosidae	Galiano 1973a
3. *Acanthoscurria sternalis*	Theraphosidae	Galiano 1973a
4. *Avicularia avicularia*	Theraphosidae	Galiano 1973b
5. *Atypus karschi*	Atypidae	Yoshikura 1958
6. *Heptathela kimurai*	Liphistiidae	Yoshikura 1958
7. (Argiopiformia)		Holm 1954
8. *Achaearanea tepidariorum*	Theridiidae	Valerio 1974
9. *Theridion rufipes*	Theridiidae	Present study
10. *Achaearanea decorata*	Theridiidae	Present study
11. *Latrodectus hasselti*	Theridiidae	Present study
12. *Segestria*	Segestriidae	Holm 1954
13. *Ischnothele siemensi*	Dipluridae	Galiano 1972
14. *Ischnothele karschi*	Dipluridae	Holm 1954
15. (Pisauridae and Lycosidae)		Holm 1954
16. *Loxosceles laeta*	Scytodidae	Galiano 1967
17. (Agelenidae)		Holm 1954
18. (Dionychae)		Holm 1954
19. *Polybetes pythagoricus*	Sparassidae	Galiano 1972
20. *Polybetes rapidus*	Sparassidae	Galiano 1972
21. *Polybetes punctulatus*	Sparassidae	Galiano 1972
22. *Polybetes pallidus*	Sparassidae	Galiano 1972
23. *Phidippus audax*	Salticidae	Taylor and Peck 1975
24. *Misumenops quercinus*	Thomisidae	Schick 1972
25. *Misumenops gabrielensis*	Thomisidae	Schick 1972

26. *Misumenops rothi*	Thomisidae	Schick 1972
27. *Misumenops schlingeri*	Thomisidae	Schick 1972
28. *Misumenops lowriei*	Thomisidae	Schick 1972
29. *Misumenops deserti*	Thomisidae	Schick 1972
30. *Cupiennius salei*	Ctenidae	Melchers 1963
31. *Loxosceles reclusa*	Scytodidae	Hite et al. 1966
32. *Octonoba octonarius*	Uloboridae	Peaslee and Peck 1983
33. *Chiracanthium inclusum*	Clubionidae	Peck and Whitcomb 1970
34. *Diguetia catamarquensis*	Diguetidae	Galiano 1969a

Vachon (1953, 1957) asserted that the true embryonal stage ends with reversion and that the stage between reversion and the rupture of the chorion was the first in a series of phases together constituting a 'larval' stage which separated the embryo from the first instar. Presumably wishing to be less than dogmatic in this proposal he also pointed out that the 'larval' stage was essentially a continuation of the embryonal process. This is reasonable, since embryonic features such as lack of appendage segmentation, lack of hairs or pigment, poor motility and in some species traces of abdominal segmentation characterize this stage (valerio 1974). However, while eyes and book lungs may be incompletely formed and no silk or sex glands are normally present, the latter are formed prior to hatching in Agelena (Purcell 1895, Strand 1906, Kautzch 1910). Extension of the post-eclosion 'embryonal' stage, through several molts in the case of the theraphosids, seems to be a feature of those spiders with the most abundant yolk reserves (Galiano 1969b), and the number and features of such stages are considered to be of high systematic value at the family level, dividing the Theraphosidae into Grammastolinae and Theraphosinae (Galiano 1973a). Several recent authors (Hydorn 1977, Galiano 1967, 1969a, 1969b, 1971, 1972, 1973a, 1973b, Yoshikura 1955, 1972) Have followed Vachon in taking the embryonal period, strictly concluding at reversion, to have a postembryonal extension until the first active instar appears. Other authors, however (Ewing

1918, Hite et al. 1966, Holm 1940, Peck and Whitcomb 1970, Juberthie 1954, Eason and Whitcomb 1965, Gertsch 1949), consider that eclosion, despite its attendant imprecision, marks the close of the embryonic period.

It is often the fate of ill-defined, variable processes to become littered with terminology and in need of a clean sweep when this begins to hamper further progress. The terms applied to developmental stages in spiders between the time egg-tooth ruptures chorion and the time the first true integument is molted are as follows:

1. Embryo
2. Postembryo or postembryonal stadia or 'free' postembryo (Holm 1954)
3. Deutovum (Gertsch 1949)
4. Exchorionate stage (Hydorn 1977)
5. Interchorional stage (Galiano 1973a)
6. Quiescent stage or quiescent nymph (Ewing 1918)
7. Prenymph (Vachon 1957)
8. Nymph (Ewing 1918)
9. Nymphal instar (Vachon 1953, 1957)
10. Prelarva (Vachon 1953, 1957)
11. Larva (Vachon 1953,1957)
12. Incomplete stadia A,B,C,D (Holm 1940, 1952, 1954)
13. Spiderling
14. First instar

Not only is the plethora of terms a problem in itself, but among the most widely accepted terms are several with unfortunately inappropriate connotations. In particular, a larva is understood by entomologists to be an actively feeding form so different from the adult (imago - another term that Vachon (1957) has applied to adult spiders) that it is separated from the latter by a metamorphosis. The spider 'larval' stage, comprising 'prelarvae' and 'larvae', differs not in gross form but only in developmental detail from the later instars, and is normally to be found not actively feeding but lying on its back and feebly waving its unsegmented legs. Terminological confusion prevents a definite assessment of whether or not spider 'larvae' ever feed. The first active instar would seem to be the first potentially feeding one; it may be necessary to repeat previous observations to resolve this problem - a most unfortunate outcome of the proliferation of descriptive terms. Nymphs in entomology are the immature forms of hemimetabolous insects, with reasonably well-defined and significant differences from the adults; spider 'nymphs' are simply young spiders. Deutovum is a specialized term in acarology, describing a particular immature form (the second egg stage) of mites. One may as well introduce such terms as 'hydatid stage' or 'tadpole' to describe stages of spider development.

It is not intended to leave the above summary as little more than a detailed complaint. After careful consideration, the following is proposed as a descriptive

scheme; it is hoped that the arachnological community will recognize it, or at least the need for something like it, and that editors will encourage future authors to present their findings in a consistent and comparable fashion. There are three guiding principles in this proposal: simplicity, the avoidance of terms with misleading connotations and the need to stick to terms already in use (to introduce any new terms would be the final irony).

First, Vachon's notion of reversion marking the close of the embryonic period is discarded. The embryo incorporates reversion as one of its developmental events. Hatching is considered the close of the embryonic stage, and is defined as the shedding (but not necessarily the total rejection) of the chorion. Peck and Whitcomb (1970) and Peaslee and Peck (1983) have defined hatching in this way. The stage between hatching and the final rejection (discarding) of the embryonic cuticle (taking the embryonic cuticle as the last of the embryonic membranes) is the postembryo stage (Whitcomb (1978) adopts this usage), and can be subdivided if required by referring to a vitellate (still enclosed by the vitelline membrane) postembryo or a cuticulate (still enclosed by the embryonic cuticle) postembryo.

If the casting of the embryonic cuticle results in an immotile stage then that stage is referred to as a quiescent instar (more than one such stage can be numbered accordingly); note that in many if not most spiders, including the subject of this thesis, Theridion rufipes,

there is no quiescent stage in this terminology because the egg membranes are not discarded until the first true integument molt, which gives rise to the first active instar. T. rufipes molts directly from postembryo to first instar and normally emerges from the cocoon as first instar. Achaearanea decorata and Latrodectus hasselti were observed to follow the same developmental pattern as T. rufipes, and these are included in Fig 2 as results of this study.

In this scheme the young of most spiders will emerge from the cocoon as first instars, defined as the first active and motile, i.e. ambulatory, stage, which frequently (but not always) arises from the first true integument molt.

Subsection 4.4.2. Developmental rate

The postembryonic period is short (Fig 1a), and the total time from oviposition to emergence is (predictably) reduced at the higher temperature.

The relative duration of the three phases (embryo, postembryo and the time from first ecdysis to emergence) alters with the temperature change. The embryonic period is completed in 0.69 of the total time to emergence at 25° C, but in 0.59 of the total time at 30° C. The relative duration of the postembryo stage remains unaltered, while the relative (and indeed the absolute) time from the first ecdysis to emergence increases. It seems, therefore, that

a faster rate of development is achieved by speeding up (not to the same extent) the embryonic and postembryonic phases but not the first instar stage.

It may be that the first instar spiderlings respond to very high temperatures by remaining in the egg sac. This would be advantageous because the spiderlings would desiccate more rapidly once out of the cocoon, owing to their increased exposure and increased activity. If this is so, moderately high temperatures may prolong the time spent in the cocoon by the first instars; this would explain the apparent increase in development time of the first instars in Fig 1a. In fact this phase is not a developmental phase in the same sense as the two earlier phases; the period from first to second ecdysis, rather than from first ecdysis to emergence, would be more comparable.

Not all spiders exhibit a single molt before emergence. According to Holm (1940) Dysderidae do not molt at all before emergence, lycosids and pisaurids molt once and salticids and thomisids twice.

It is not clear why the embryo and postembryo stages respond differently to a temperature increase of 5° C from 25° C, the embryo stage reducing its relative development time by twice the amount that the postembryo does. These differences may relate to the overwintering strategy of this species and/or its congeners where they occur in temperate zones. A stronger response from eggs than from postembryos suggests egg overwintering, but most spider

species do not overwinter in the egg stage (Foelix 1982).

Only limited reliance can be placed in the developmental threshold values of Fig 1b, derived as they are from but two temperature points in each case, especially in view of the fact that no development took place at 20° C. A comparable study on the related theridiid Latrodectus hasselti showed a lower threshold for embryos than for postembryos, i.e. the embryos would develop at 18° C but the postembryos would not. In addition, the postembryos would develop at 20° C but first instars would not (Downes 1986). This 'switching' threshold sequence does not seem to occur in Theridion rufipes; It appears that a common threshold close to 12° C applies to both embryos and postembryos. Clearly, there are differences in the developmental strategies between these two theridiids.

However, some overriding mechanism, shutting off development at about 20° C, may be superimposed on the developmental trends suggested by Fig 1b.

In temperate regions T. rufipes could be expected to develop (slower) at temperatures down to 10° C or below, as does Latrodectus hasselti from temperate zones (Forster 1984). Speculation on why this does not occur in tropical populations may not be very helpful at this stage, but over the five years of this study the mean monthly temperature in this district of Townsville has only fallen below 19° C in one two-month period (June and July 1982), when it sank to 18.3° C. Minimum temperatures do occasionally go below 10° C during some nights of the

cooler dry season, but corresponding day temperatures on these occasions are likely to be in excess of 20° C.

A temperature cycle of 15-25° C, evenly changing over a 24-hour period, may produce a very different outcome from a constant 20° C regime, despite the former's mean value of 20° C. It would be interesting to see whether such a cyclic temperature regime also showed that development times could be predicted by day-degree values above 20° C.

The production rate of egg sacs is also markedly affected by a reduction of 5° C from 25° C, as Table 4 shows. Fecundity and fertility are not significantly affected (see Chapter 7) but oviposition intervals are greatly extended. Undoubtedly, as with the effects of temperature on early development, the explanation for this apparently near-limiting effect of an unexpectedly high temperature is to be found in the temperature cycles of the animal's natural environment, correlation of the latter with food availability, and hence with prospects for successful development to maturity.

Plate 10.

(a) An undeveloped egg among postemb yos.
Note the crumpled chorions stil
attached to the abdomens of some
individuals (x 1)

(b) First instar spiderlings feeding on
an egg and on a sibling x20)

Chapter 5. OOPHAGY - THE INVESTMENT

Section 5.1. Introduction

In this chapter the concept of oophagy in arthropods is briefly reviewed and is discussed in detail with respect to spiders. Its occurrence in T. rufipes is recorded and data is given on the probability of development of T. rufipes eggs in relation to their size.

Wilson (1971) gives many examples of oophagy (egg cannibalism) and the use of trophic eggs, mostly from among the Hymenoptera. He implicitly (but not explicitly) distinguishes between the phenomena, trophic eggs being invariably infertile and being produced solely as a nutrition source. However, while a fertile egg cannot be trophic, an infertile egg need not be trophic either, unless its production is due to an evolved strategy for the provision of extra nourishment by this means. In practice it is difficult to determine whether eggs used as food were fertile or not.

Ho and Dawson (1966) found that differences in cannibalistic behaviour - especially that of larvae upon eggs - had a profound influence on competitive superiority of the flour beetle Tribolium castaneum over T. confusum in culture, and the use of the term cannibalism implies that these authors do not consider the food eggs as trophic. Similarly, Eickwort (1973) reported cannibalism

of unhatched eggs, leading to an increase in fitness that shows the trait would be selected, in the chrysomelid beetle Labidomera clivicollis. One of the many further studies on Tribolium was that of Mertz and Robertson (1970) who showed that egg cannibalism in Tribolium reduced the mortality of the cannibals and increased their development rate.

Egg-feeding, however, is best documented for the Formicidae where the distinction between trophic eggs and other inviable eggs is more easily made. A newly mated queen ant of the species Solenopsis invicta, for example, lays two clearly different types of egg, small and large; the large ones are a food supply for larvae that hatch from the small ones (Glancey et al. 1973). Queens of Pheidole pallidula produce trophic eggs for workers and larvae before leaving the nest for the nuptial flight (Passera 1978). The level of juvenile hormone, influenced by the nutritional state, is implicated in the production of trophic (unembryonated) eggs by unmated Solenopsis invicta queens (Voss, 1981). Workers, too, may lay trophic eggs (Brian and Rigby 1978, Torossian 1979).

If unfertilized eggs, not 'designed' as trophic as they are in some ants, are produced fortuitously by flour beetles or chrysomelids or spiders (Plate 10a), and the developing young feed on these eggs, the result is at least the functional equivalent of the production and use of trophic eggs. Three basic alternatives therefore exist: use of trophic eggs, opportunistic feeding on infertile

eggs, and egg cannibalism. It may be that more than one of these operates in any given instance. No evidence is available, from this study or any other, that any of the eggs produced by spiders are trophic eggs of the kind laid by some ant queens. The absence of such evidence does not, however, preclude the possibility.

A previous study of inviable eggs in spider broods found that in Latrodectus geometricus in western central Africa the mean total loss was 31% comprising 3-4% infertile, 13-15% fertile but inviable and 8-9% lost in diapause (Bouillon 1957a). Late hatching eggs, those in diapause and even those in the act of hatching were all utilized as food by the developed spiderlings.

A number of authors have commented on the occurrence of undeveloped eggs in spider broods. Kaston (1970), for instance, observed that in Latrodectus "Naturally one could hardly expect that all the eggs laid would actually develop. Very few sacs showed a development of 100% of the eggs." And Peck and Whitcomb (1970) noted that 10% of the eggs in egg masses of Chiracanthium inclusum failed to develop due to unknown causes. A consideration of the causes, however, is pertinent to the present study. The list below sets out the possible causes, with comments. Infertility is not included as it has already been noted above.

1. Lack of sufficient yolk (would probably develop at least to a stage at which its original fertility was evident)
2. Lack of some essential accessory factor (congealed mass effect noticed by Bonnet (1935) in Theridion tepidariorum sacs; he suggests lack of the viscous coating substance. Congealing of egg clumps not uncommon in the present study)
3. Damage - from extrinsic sources (interference in web, e.g. by a predator. Also activity of captured prey struggling in web)
4. Damage - from intrinsic sources (whether late-hatching eggs may be ruptured, pressured or otherwise damaged by early developed young is unknown)
5. Genetic insufficiency (the catch-all category - i.e. 'other')

Section 5.2. Materials and methods

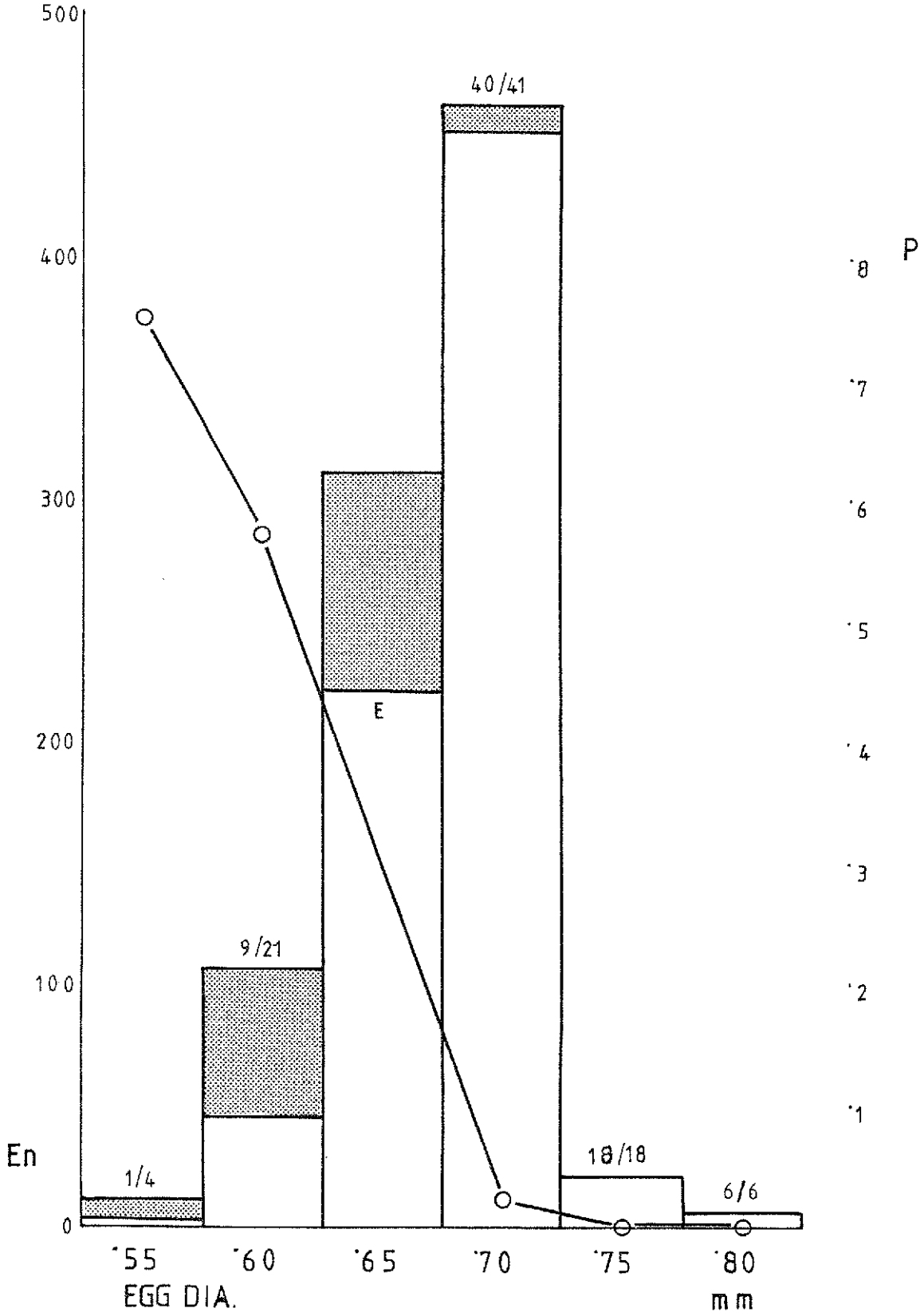
The methods described in section 4.2. permitted egg-feeding to be observed, but photographic records of these events were difficult to obtain because spiderlings would disengage from feeding during transport from the laboratory to the photomicroscope. The empty, usually cup-shaped, chorions found within abandoned egg sacs (Plate 3b) were produced by feeding. However, if the spiderling

did not consume all the contents of an egg it fed upon, the remaining yolk became discoloured brown, presumably through the action of enzymes secreted for preoral digestion, and often became difficult to distinguish from degenerated eggs that had not been fed upon.

To investigate variation of yolk content in the eggs a stage micrometer-calibrated graticule was employed in the measurement of egg diameters using a stereo microscope. A total of 915 eggs from 26 egg sacs were measured to the nearest 0.05 mm. 90 eggs of different diameters were marked (by noting their position, not by physically marking them) to test whether successful development was in any way related to egg size. Eggs 'marked' for such purposes were never handled; the cocoon silk was merely teased away to reveal part of the egg mass within, and only those eggs whose superficial location made the whole diameter visible were measured. Most often this proceedure did not reveal eggs of differing diameters. Any disturbance after 'marking' changed the relative positions of the eggs, rendering the identification (i.e. location) of the 'marked' eggs unreliable. Unfortunately it was not possible to conduct every trial under an undisturbed microscope, and all the 'marked' eggs of 0.65 mm dia. were displaced by slight movements. Limited trials under undisturbed microscopes or further repetitions of the trials as conducted would have made good this shortcoming.

Fig 3. Egg size, proportional fertility and probability of failure to develop. En= numbers of eggs (columns - clear portions, fertile; stippled portions, infertile). P= probability of failure to develop (single line). Eggs of diameter 0.65 mm were not assessed for proportional fertility (see section 5.2), so probability of failure to develop is not plotted for that diameter, and proportional fertility is estimated (E) from the point at which the failure probability line crosses the 0.65 mm mark.

Values given above columns are fertile eggs/total sampled for fertility. The column subdivisions are based on these ratios.


500
400
300
200
100
0
En
P
·8
·7
·6
·5
·4
·3
·2
·1
40/41
9/21
E
1/4
18/18
6/6
·55
·60
·65
·70
·75
·80
EGG DIA.
mm

Section 5.3. Results

Postembryos were never observed to feed on eggs and are in fact incapable of doing so. First instar spiderlings, on the other hand, not only fed on eggs but did so voraciously almost from the earliest moment after ecdysis (Plate 10b), their abdomens darkening to almost black with the excess consumption of a large amount of egg material, just as excess uneaten yolk left in a half-eaten egg darkened after feeding. Spiderlings of T. rufipes occassionally fed on late-developing siblings as well as on undeveloped eggs (Plate 10b).

Eggs that were not consumed within a few days after the appearance of the first instar spiderlings were usually left untouched thereafter. This is surprising when it is realized that undeveloped eggs are an attractive food source for adults as well as young. Hite et al (1966) observed that adult female Loxosceles reclusa sometimes fed on their own eggs; and on one occasion during the present study an adult female T. rufipes fed on the egg mass of a sac of hers that had been accidentally squashed.

Up to three spiderlings have been observed to feed simultaneously on a single egg, but one spiderling to an egg was the most frequent situation. It is not known how long it normally takes for a spiderling to drain an egg of its contents, but the process has been observed in two cases to continue for two hours without completion. Towards the end of the feeding process the almost-empty

chorion took on the appearance of a bowl into which most of the spiderling's cephalothorax was inserted.

When the fertility rate was low and there were many eggs for the spiderlings to feed upon, more than one egg was often consumed by each spiderling, and the distension of the abdomen of such spiderlings could reach alarming proportions, so much so that these spiderlings were sometimes unable to hang on silk threads, but fell to the bottom of their containers.

Egg sacs that were 'overdue' for the emergence of the spiderlings were often found to contain just a few heavily-fed spiderlings among a large number of full and empty undeveloped eggs. The same thing was reported by Kaston (1970) for Latrodectus.

That egg-feeding is, like hatching and molting, not without attendant risks is evidenced by the occasional discovery of spiderlings stuck by their chelicerae to a gluey mass of yolk, within egg sacs since abandoned by the other spiderlings.

The eggs proved on measurement to be non-uniform in diameter, ranging from 0.55 to 0.80 mm (Fig 3). Eight of the 26 egg sacs sampled contained eggs of diameter 0.70 mm only. Thirteen sacs contained eggs spanning two of the diameter values and five sacs contained eggs spanning three diameter values.

The mean diameter (in mm, with standard errors) of fertile eggs was 0.71, s.e. 0.006 (n = 74). That of infertile eggs was 0.60, s.e. 0.008 (n = 16). Smaller eggs

were significantly less likely than larger eggs to develop successfully (the log-likelihood statistic G, using Williams' correction, gave a value of 36.87 with 4 degrees of freedom. From chi-square tables, $p < 0.001$)

Section 5.4. Discussion

The phenomenon of egg-feeding is itself easily overlooked even by competent observers. Shulov (1940) reported a fertility rate of 85% and 95% in broods of Latrodectus tredecimguttatus and L. pallidus respectively, and noted elsewhere in the same paper that "The comparison between the results obtained with the speed of mortality of the young spiders which remained in the sac and died there shows an astonishing difference (12-19 days emergents against 110-139 days stayers). We must keep in mind that the young spiders do not devour each other inside the cocoon, and thus lack any kind of food."

A glance at Fig 2 will show the scope for confusion when labels like 'postembryo', 'first instar', 'deutovum' and such like are applied to the developmental stages 'with gay abandon' (Peck and Whitcomb 1970). It is therefore not surprising that the records of observation of egg-feeding by early stage spiderlings inspire something less than total confidence. To confuse matters further, it seems that postembryos of some species, although incapable of feeding for a day or two after eclosion (during which time they are able only to flex

their tarsi), develop motility and co-ordination enough to feed on unecloded eggs prior to their first true molt (Taylor and Peck 1975). This observation led these latter authors to assume that earlier investigators may have been mistaken in their opinions that the newly-hatched spiderlings never fed (Kaston 1948), and also to assume that where feeding had been observed (Kaston 1970, Peck and Whitcomb 1970, Galiano 1969a, Schick 1972) it was indeed the newly-hatched individuals that were feeding.

A similar interpretive difficulty arises from Valerio's (1974) assertion that "This feeding activity has been directly observed only in the first instar (i.e. before the first true molt), leading many workers to suppose that egg-feeding takes place only in this instar." This statement would seem to be the very opposite of Taylor and Peck's (1975) idea of what earlier authors were saying. In fact Kaston's (1970) first instars were not the stage prior to the first true molt, to give only one instance of misinterpretation. Valerio (1974) goes on to say that literature reports (Juberthie 1954, Bouillon 1957a, Kaston 1970) of feeding on eggs by 'first instar' theridiid spiderlings (Valerio's 'first instar' = most others' postembryo) appear to be errors, and that feeding is only done by "second instars not quiescent instars". Of course, Valerio's first instars were quiescent, but Kaston's weren't.

Schick (1972) has also asserted that "Several investigators have noted, however, that (the deutovum)

will feed upon undeveloped eggs..."; this is likely to be an error of interpretation. It may not be an error, nor may any one of the other authors' statements, but these reports taken together are irreconcileable - somebody must be wrong. What can be reliably stated is that unecloded eggs and late-hatching siblings are harvested by developed spiderlings, and that this harvesting is probably carried out by the first developmental stage functionally capable of such feeding. In T. rufipes and the three related local theridiids also mentioned in this study, this is invariably the first instar (as defined in subsection 4.4.1), a situation very likely to be typical of the theridiids.

The alimentary development of postembryo stage spiderlings and probably many if not most quiescent stages may preclude feeding altogether. Yoshikura (1955) determined that the alimentary canal of Heptathela kimurai (a liphistiid) was fully open after hatching but still contained yolk debris. The digestive tract of Achaearanea tepidariorum on the other hand is still full of yolk (making feeding unlikely if not impossible) at the post-hatch stage, and such a condition is probably normal for all theridiids (Valerio 1974).

Feeding on late-developing siblings was also reported for Octonoba octonarius by Peaslee and Peck (1983) and for Misumenops spp. by Schick (1972) who suggested that only liquid digestion was possible because no enzymes were available for preoral digestion, so less nutrition could

be gained by eating postembryos. T. rufipes postembryos glisten and are sticky, and are rarely eaten by first instar spiderlings; they may be protected to some extent against cannibalism by being distasteful to their voracious elder siblings. Schick (1972) made the same observation on the postembryos of Misumenops.

Egg diameters are highly variable (Fig 3) and size appears to be strongly correlated with viability. If fertile egg diameters are normally distributed with a mean of about 0.7 mm (Fig 3) then undersize, inviable eggs can be visualized as a superimposed addition to a basically 'normal' distribution.

Most egg-feeding was upon eggs which apparently had not developed at all, rather than on partly-developed individuals. This suggests either that small eggs are less likely to be fertilized or, if inviability does not arise from infertility, that developmental failure occurs very early in the developmental process. An additional relevant point is that egg sacs of very low fertility, i.e. containing a large excess of 'food' eggs, were not uncommon, and egg material has a high energy content relative to the female (Anderson 1978). One egg sac in the present study contained 116 undeveloped eggs and but a single first instar spiderling; this extreme case emphasizes the resource wastefulness of producing excess 'food' eggs and suggests that it is probably not a trophic strategy parallelling that found in the Hymenoptera.

It is not known why many eggs remain uneaten if not fed upon within a few days of ecdysis; normally the spiderlings would be leaving the egg sac two to three days after the molt and this may be relevant to their abstention from egg-feeding when confined along with undeveloped eggs for longer than the normal molt-emergence period.

Another problem concerns the late emergence of heavily engorged spiderlings. If extra early nourishment obtained from infertile eggs allows spiderlings to travel further and escape unfavourable habitats, relatively late emergence after excess egg-feeding would seem contradictory. However, the amount of extra starvation resistance time gained as a result of substantial egg-feeding (detailed in Chapter 11) is usually very large compared to the time 'wasted' through delayed emergence.

Chapter 6. FECUNDITY AND THE EGG SAC SEQUENCE

Section 6.1. Introduction

Measuring fecundity and fertility over the oviposition sequence of Theridion rufipes was one primary aim of this study. The direct relationship between fecundity and fertility, irrespective of other factors, may also have an ecological interpretation. If unfavourable environmental conditions lead to lower fecundity they may also lead to lower fertility. This may well be predicted if a food shortage was the prime malfactor. However, well-fed spiders whose environment was unfavourable for other reasons may be highly fecund but still may be found to produce relatively few viable eggs.

A potential source of bias in the results was the possibility that fecundity (i.e. sac fecundity) correlated with egg sac production rate. Highly fecund individuals might produce more egg sacs than less fecund individuals, or there may be a compensation effect such that increased rate of production of egg sacs results in fewer eggs per sac. Correlation tests were carried out to test these effects.

T. rufipes is typical of theridiids in being highly fecund and iteroparous. Some spider species decrease fertility or batch size with successive egg cocoons, but others do not. Among theridiids, for example, Achaearanea lunata exhibits a fecundity decrease with successive

ovipositions (Toft 1978) while Synotaxus turbinatus does not (Eberhard 1979); Theridion tepidariorum becomes progressively less fertile with successive ovipositions (Bonnet 1935) while Latrodectus mactans does not (Kaston 1970).

Patterns within a species may also be extremely variable. Evidence of any real changes with parental age may require large sample sizes, especially if reproductive success is affected by the spiders' feeding habits between ovipositions (Austin 1984).

Section 6.2. Materials and methods

Egg sacs from field and laboratory dwelling spiders were collected as described in Chapter 2. It was not always possible to keep track of particular females in the field because adult T. rufipes are active at night and sometimes change their locations. While this problem cannot be entirely overcome, where any doubt arose as to whether an egg sac was a first sac the sac sequence number of that and all subsequent sacs of that female were coded as unknown.

Those egg sacs whose sequence number was known were used as the data set for this chapter, a total of 707 sacs produced by 211 females, both field and laboratory specimens. Fewer egg sacs were of course obtained for the later sacs of the sequence. Less than ten cases were obtained for egg sacs ten to twelve, the latter maximum

sac productivity being attained by only a single female.

The primary analysis of variance involving variations over the sac sequence (SACNO) (see Chapter 3)) was a four-way analysis including feeding rate (FEEDST), FOODTYPE and ORIGIN. A one-way analysis was also carried out, along with a test for least significant difference at the 0.05 level. The one-way analysis permitted the use of twelve groups (one for each sac of the sequence to the maximum recorded), whereas the four-way analysis necessitated the coding of the sac sequence into four groups of three sacs each.

The relationship between mean sac fecundity and number of sacs produced was tested to determine whether the more sac-fecund individuals tended to produce more or less sacs than those females not so fecund.

Section 6.3. Results

The one-way ANOVA of the sac sequence (SACNO), with 11, 695 (i.e. treatment, residual) degrees of freedom, gave F values and significance levels as follows:

Fecundity	2.584	0.001	(4)
INVIA 1	1.634	0.085	(3)
INFERT	1.410	0.163	(2)

The bracketed figures are the percent amounts of the total variance explained by variability between sacs, for

this one-way test. If a critical level of 0.05 or 0.01 is applied, these values are interpretable in the same way as those resulting from the four-way ANOVA (Table 2). Nonetheless, there are considerable differences between the two sets of results.

With respect to fecundity, a least significant difference test at the 0.05 level showed that the third egg sac was significantly different from the first; the tenth sac from all others except 9, 11 and 12; and the eleventh sac from all others except 10 and 12. The mean values and standard errors are presented graphically in Fig 4a.

The relationship between sac fecundity and productivity, which was noted above as a potential source of bias, is given in Table 5. For the correlation values to be meaningful they had to be computed for cases where (a) temperature was fixed (b) feed rate was the same and (c) the sac sequence was uninterrupted by missing data or experimental error. These limitations led to a low number of cases (n) for each computation. The variables used in the correlations were mean sac fecundity and numbers of egg sacs produced per unit time.

Table 5. Correlation coefficients for single-sac fecundity vs. egg sac production rate.

Feed rate	temp,° C	n	cor. coeff.	sig
Maximal	20	7	0.03497	0.470
Minimal	20	7	0.06888	0.442
Maximal	25	9	0.32646	0.196
Minimal	25	9	0.22847	0.277
Subminimal	25	5	0.02070	0.487
Maximal	30	10	0.50182	0.070
Minimal	30	8	0.34289	0.203

None of the correlations of Table 5 are significant at the 0.05 level. It is concluded from these results that the number of eggs a female T. rufipes produces is independent of her mean sac fecundity. This result was further checked by calculating the mean sac fecundity of only those females that produced nine sacs or more. This mean value was 120.7 (the mean for the entire data set of Fig 4a was 114.6), and these females showed the same trend through the sac sequence as did the whole data set.

Fig 4b shows the values for the three formulations of infertility with respect to the egg sac sequence. The apparent trend towards an infertility increase in later sacs of a sequence involves relatively few cases for those later sacs and is not confirmed by statistical tests. Four-way and one-way analysis of variance (see above and Table 2) have shown no significant differences in

infertility between the sacs.

Table 4 gives a mean oviposition interval of 16.1 days at 25° C, and a mean mating-oviposition time of 6.6 days. From this, a time of about 184 days for a twelve-sac sequence can be inferred. The female that produced twelve sacs did this in 136 days (at 25° C) plus the (unknown) mating-oviposition time. So sperm in T. rufipes can remain viable for at least some 143 days after a single mating and can be used in the production of at least twelve egg sacs. The total number of eggs produced by that female was 1535.

Section 6.4. Discussion

In most spider species a single mating can probably provide enough sperm for the entire reproductive life of the female. Bonnet (1935) determined that in T. tepidariorum a single coitus lasting 5-6 seconds provided sperm enough to fertilize 3000 eggs, although he also found that sperm longevity may fail if winter interrupts the oviposition cycle. From the male's point of view, sperm priority is all-important where single-mating sufficiency prevails among unsociable individuals. Female theridiid spiders have conduit reproductive anatomy (Figs 5a and 5b) that favours first male sperm priority with all its attendant behavioural and physiological patterns of self-interest (Austad 1984).

Kaston (1970) was of the opinion that depletion of

viable sperm reserves over the normal oviposition sequence of the female was unlikely (at least for Latrodectus), and Austad (1984) pointed out that there was no evidence that sperm deterioration within spermathecae was a significant factor in the evolution of multiple mating systems in spiders. Year-long sperm storage is routine in Atypus affinis (Bristowe 1958), 'tarantulas' (Baerg 1958) and Trite auricoma (Forster and Forster 1973).

As was the case with L. hasselti (Downes 1985), the present results for T. rufipes lend no support to the idea that fecundity decreases over a sac sequence. On the contrary, fecundity for the the later sacs appears from Fig 4a to be greater than that for the earlier ones, and the least significant difference analysis showed these values to be significantly higher than the others. This adds a new dimension to the often-raised question of whether female spiders normally maintain their fecundity levels or become less fecund with age. An increased fecundity in later egg sacs would be beneficial if the female became progressively less likely to construct further egg sacs or became more likely to produce infertile eggs. The increased likelihood of death with increasing age is probably not a significant factor if that likelihood of demise reflected an increasingly debilitated physiological condition resulting from aging. Limited longevity of sperm, leading to increasing proportional infertility, may well result in an increased reproductive effort in the later part of the female

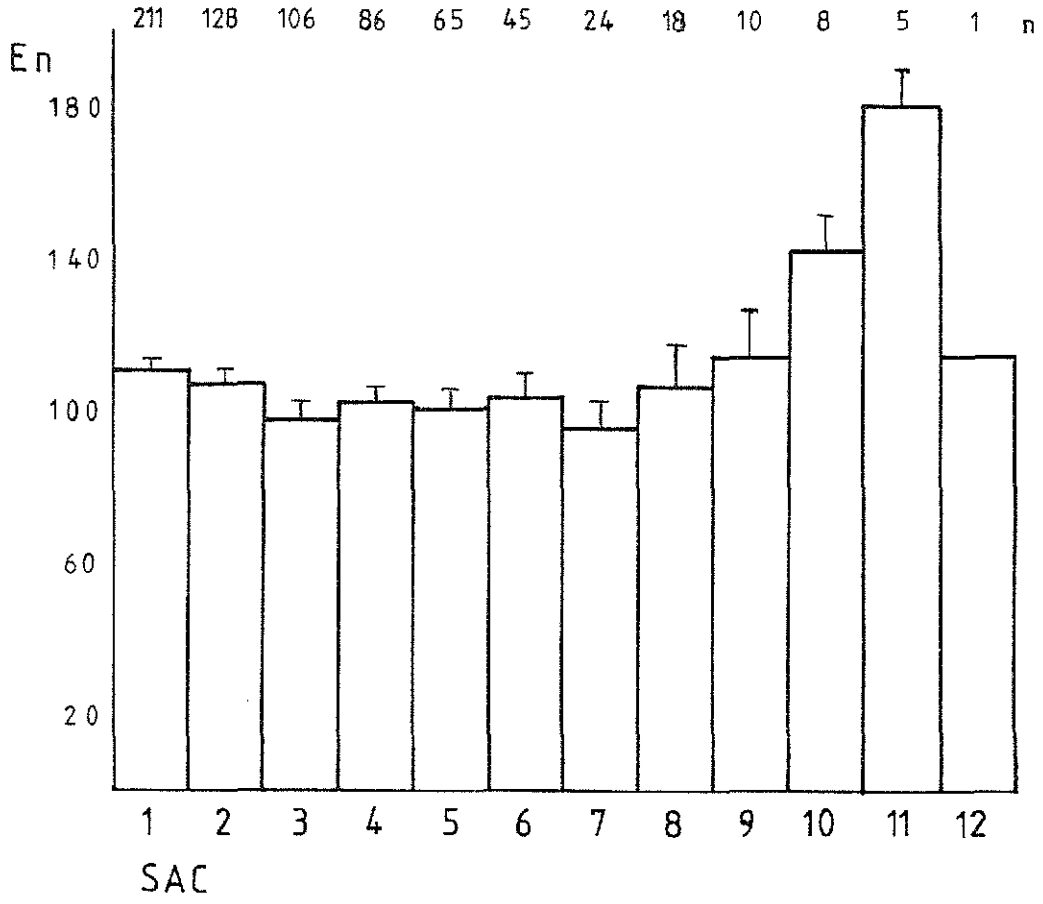
spider's egg-producing lifetime, if sperm was not limited by quantity available but was likely soon to become ineffective. The results of this study give no evidence of this, but Figs 4a and 4b suggest that further investigation along these lines may prove fruitful.

A progressive decrease in fertility, however, where it occurs, may not necessarily be a maladaptive strategy. In Phidippus johnsoni the later egg sacs of the sequence, with numerous undeveloped eggs available to nourish the spiderlings before they emerge from the cocoon, are produced (perhaps as an alternative to providing more yolk per egg) at a less favourable time of year when the dispersing spiderlings may find the climate less benign and their first meal less easily obtained (Jackson 1978). This could be seen as a special case of what is perhaps a more general principle - that a beneficent environment and/or favourable circumstances (especially in terms of nourishment but also involving a number of other factors) will maximize the number of young produced and minimise the proportion of infertile or otherwise inviable 'trophic' eggs, and that unfavourable circumstances will result in the reverse. This question is not resolved here.

Fig 4a. Fecundity over the egg sac sequence. Column values supplemented by standard errors. En = mean number of eggs per sac. n = number of sacs examined.

Fig 4b. Proportional inviability and infertility over the egg sac sequence. Whole column heights represent INVIABILITY 2 (failure to hatch) for the three sacs (9, 10 and 12) where this value differed from INVIABILITY 1 (failure to develop). Whole column heights for other sac nos., and whole column heights less stippled portions for sacs 9, 10 and 12, represent INVIABILITY 1. Dark portions represent INFERTILITY (undeveloped eggs, full or consumed). n is as for Fig 4a.

(a)


211 128 106 86 65 45 24 18 10 8 5 1 n
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180
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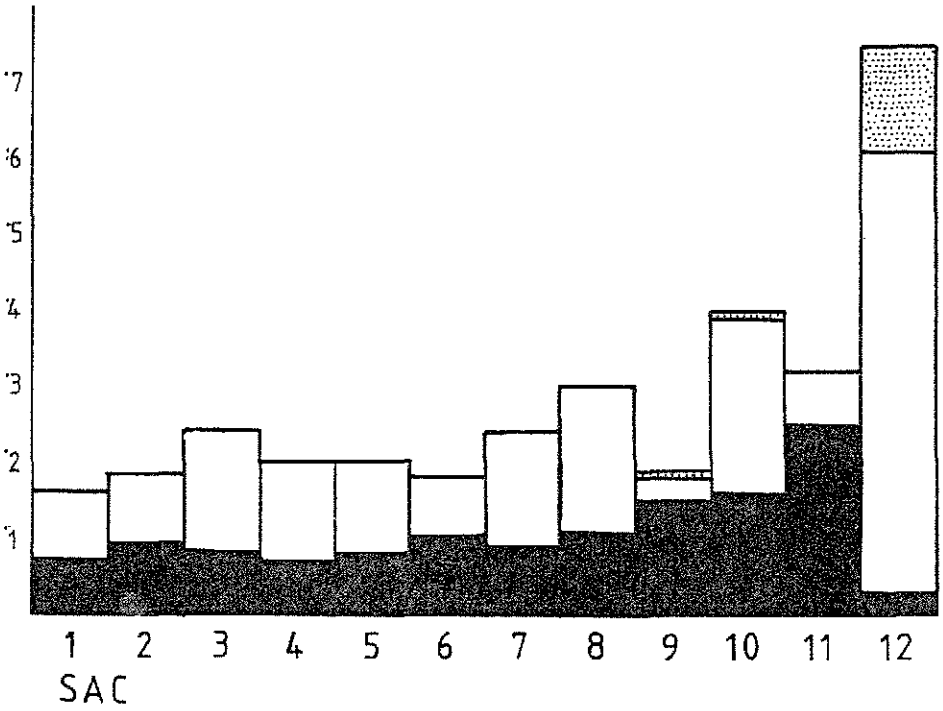
SAC

(b)


7
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SAC

Fig 5. Cul-de-sac (A) and conduit (B) reproductive anatomy in spiders. CD = copulatory duct

E = epigyne

FD = fertilization duct

G = gonopore

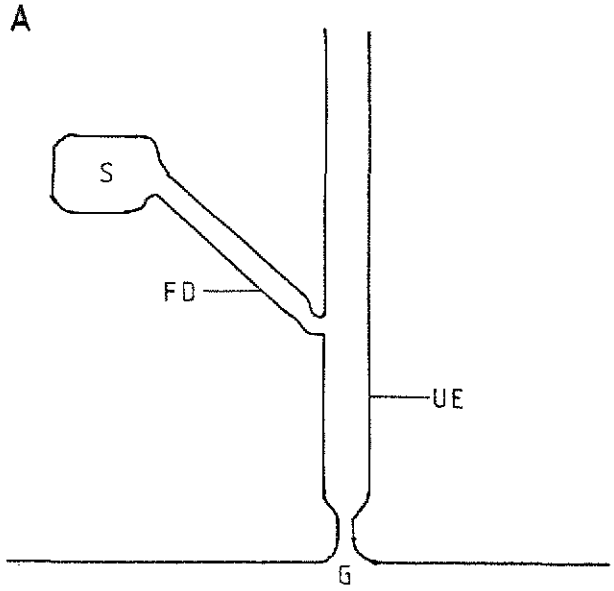
GO = genital opening

S = spermatheca

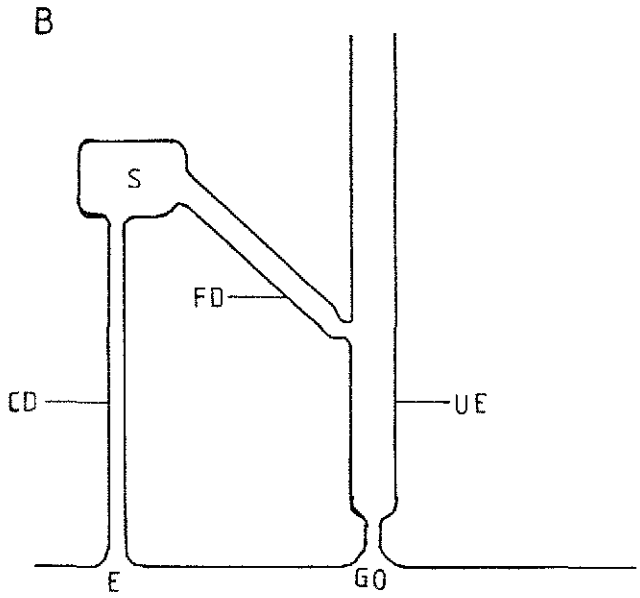
UE = uterus externus

Diagrammatic

A



B



Chapter 7. TEMPERATURE EFFECTS

Section 7.1. Introduction

If optimum environmental conditions are conducive to maximum fertility in female spiders, temperature variation (a major component of environmental conditions) might produce a corresponding variation in fertility. This chapter details those aspects of the study that addressed this question. There were two main intentions. First, to evaluate the effect of constant laboratory temperatures upon the reproductive variables of interest, and second, to see whether a seasonal trend in these reproductive variables existed for Theridion rufipes in the field. It was not assumed that any such trend would necessarily reflect the direct effects of changing seasonal temperatures.

T. rufipes lives and breeds throughout the year in Townsville, where temperatures may range from a midwinter night low of less than 10° C to a midsummer day high of 40° C or more. It is not known to what extent, if at all, T. rufipes is able to avoid temperature extremes by selection of the most suitable web sites.

Although there have been numerous studies of the effects of temperature on the behaviour, physiology and development of spiders, temperature effects have not figured in the few investigations into the proportional occurrence of infertile eggs.

Section 7.2. Materials and methods

With respect to temperature the female spiders under study can be divided into six groups:

1. 18 kept in the laboratory at a constant temperature of 30° C
2. 32 kept in the laboratory at a constant temperature of 25° C
3. 17 kept in the laboratory at a constant temperature of 20° C
4. 56 kept in the laboratory at room temperature (air conditioned, 22-26° C)
5. 126 free field specimens subject to prevailing outdoor temperatures
6. 27 captive field specimens, temperature regime unknown but subject to prevailing outdoor temperatures

The females of group four will not be included in the results of this chapter because a 4° C variation, though not very great, introduces imprecision over that temperature range (20-25° C) which has already been shown to have marked effects on T. rufipes in other ways. The last two groups are separate because the microclimate of the glass tubes used for confinement may have made the temperature regime differ significantly from that experienced by non-captive specimens. Individuals of group

six were confined so that satisfactory 'runs' over the egg sac sequence could be obtained at field temperatures; free field specimens often sufered death or displacement after producing only one or two egg sacs, or the identity of such specimens became uncertain and they therefore had to be excluded from further involvement in the study.

Groups five and six contained females first observed as subadults (see Chapter 2). Females adult when first observed (perhaps including females originally of group five but since displaced) also provided egg sacs (totalling 35) for this aspect of the study; such egg sacs were coded with female no. not applicable and sac no. unknowwn. By appropriate specification of missing values, subsequent SPSS analysis used these sacs only as accessory data for group five. In addition, first egg sacs produced in the field by females that were then collected for laboratory studies are also accessory data for group five. These latter females are included in the number of cases specified above for group five.

For each fixed laboratory temperature, a photoperiod of 14/10 hours light/dark was used. Early trials at 20° C resulted in consistently high proportions of egg infertility, and it was suspected that the original ratio of viable to inviable eggs produced by the female was being obscured by the fact that few eggs developed at all at a sustained temperature of 20° C. Subsequently, egg sacs produced at 20° C were transferred (usually within a day, never later than three days after oviposition) to 25° C for

incubation. In this study, therefore, it is the temperatures experienced by ovipositing females which are being examined.

Mean monthly temperature and rainfall data for the district under study were obtained from James Cook University's Geography Department for use with field results.

Section 7.3. Results

It has been stated above (Chapter 3) that temperature was one of the variables that contributed negligibly to the total variance observed in fecundity and fertility. All of the results of this section confirm that within the observed range of temperature of the study, fecundity and fertility did not show any relationship to temperature.

For the fixed laboratory temperatures of 20, 25 and 30° C, Fig 6 summarizes the data derived from 307 egg sacs. From this it can be predicted that prevailing field temperature will not correlate with fecundity or fertility in egg sacs collected in the field. Fig 7a confirms this expectation.

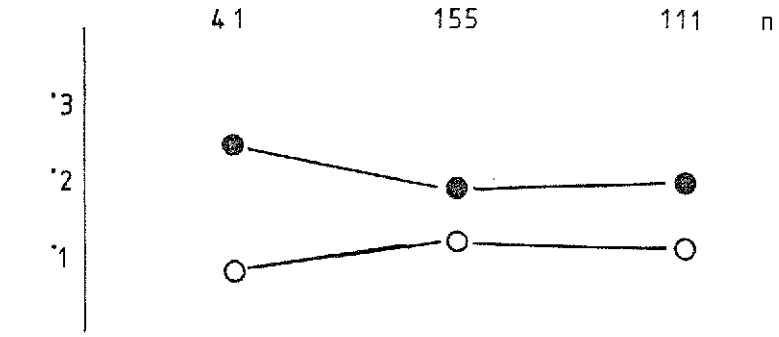
Field sacs from free spiders were collected in 28 of the months over which the study ran. There was no correlation between the values for fecundity, inviability and infertility of egg sacs collected in each of those months and the appropriate mean prevailing monthly

temperatures (r = -0.154, -0.245 and -0.158 respectively). In view of these values, a complete year-by-year graphical presentation of the data was considered unnecessary, and Fig 7a represents the pooled data, with mean monthly temperature values averaged from those of the successive years (the variation between these means was very small; 4° C was the maximum difference in any one case, and standard errors ranged from 0.52 to 0.86)

Since insect abundance, and consequently food availability for the spiders, may be correlated with rainfall, the data were examined for correlation between reproductive variables and rainfall. Correlation coefficients for fecundity, inviability and infertility in these cases were 0.053, -0.068 and -0.069 respectively. Nor was there any correlation between the reproductive variables and the rainfall levels of the previous month rather than those of the month corresponding to the collection of the egg sacs concerned (r = -0.009, -0.094, 0.006).

The values given in Fig 7b, for the 106 egg sacs produced by field-captive specimens, clearly do show seasonal change. The reason for this cannot be explained with the present data. It may be that confining females in this way affected the early egg sacs produced, but temperatures in the tubes may also have been higher than outside them.

Fig 6. Mean fecundity and mean proportional inviability and infertility in relation to temperature. Column values (fecundity) supplemented by standard errors. Black dots, INVIABILITY 1 (failure to develop). Open dots, INFERTILITY (undeveloped eggs, full or consumed). En= mean number of eggs per sac. n= number of egg sacs examined.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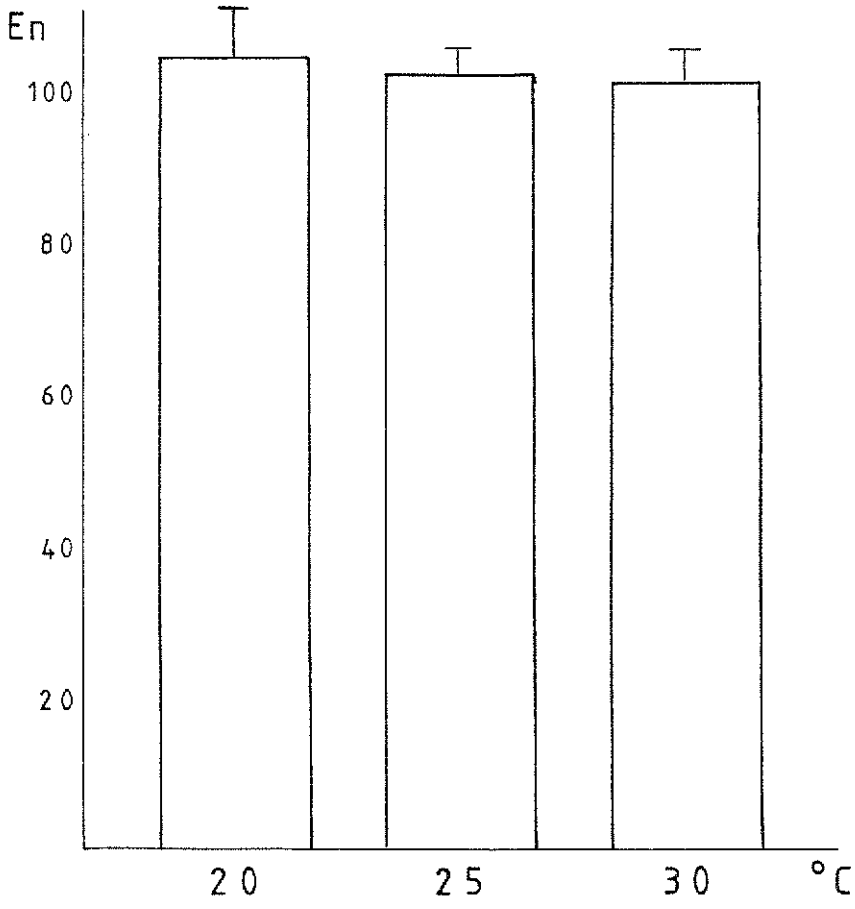
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Fig 7a. Mean monthly fecundity and mean proportional inviability and infertility, field-free specimens. Column values (fecundity) supplemented by standard errors. Black dots, INVIABILITY 1 (failure to develop). Open dots, INFERTILITY (undeveloped eggs, full or consumed). Crosses, mean monthly temperature (see section 7.3). En= mean number of eggs per sac. n= number of egg sacs examined. T= temperature (° C).

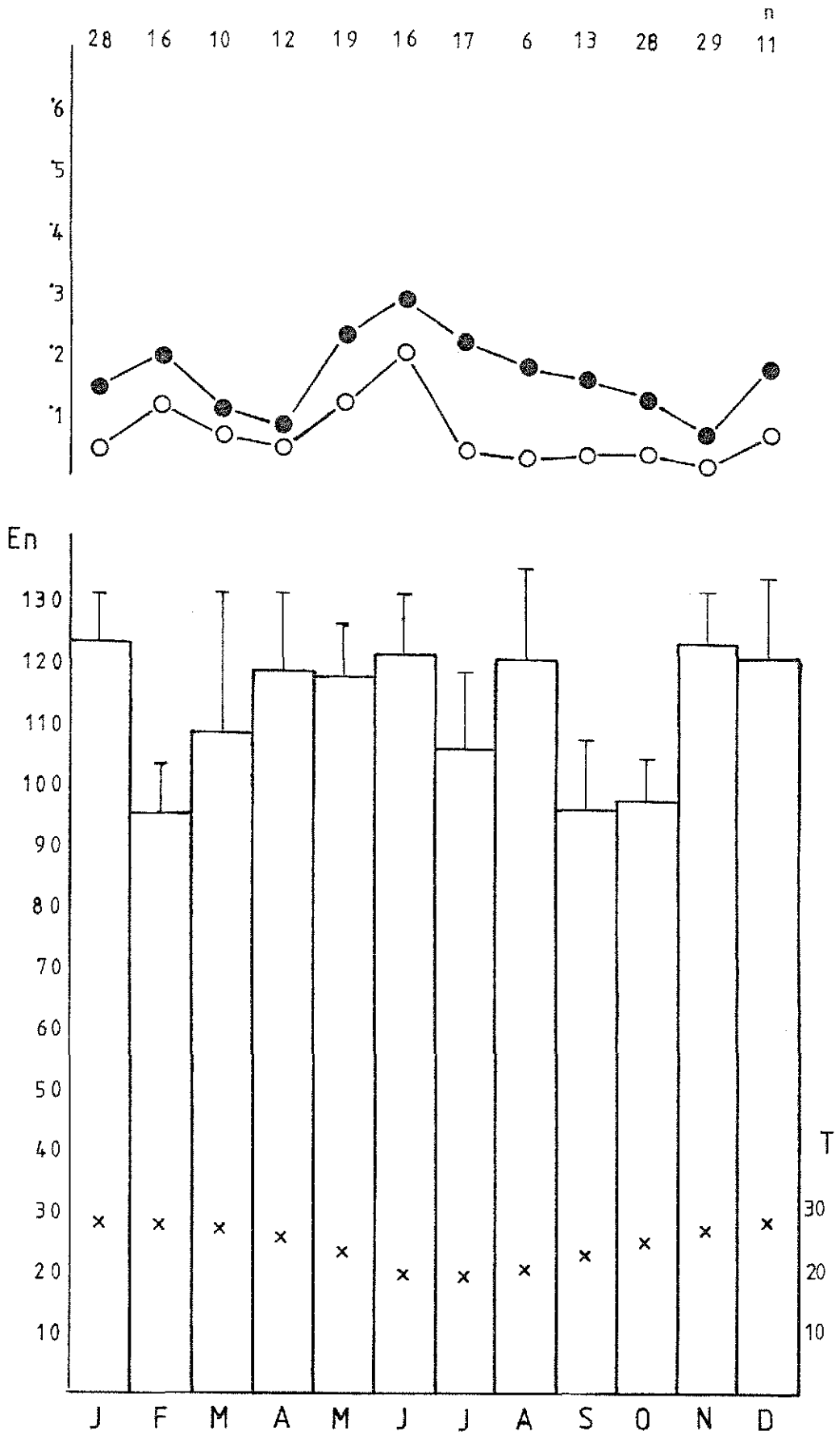
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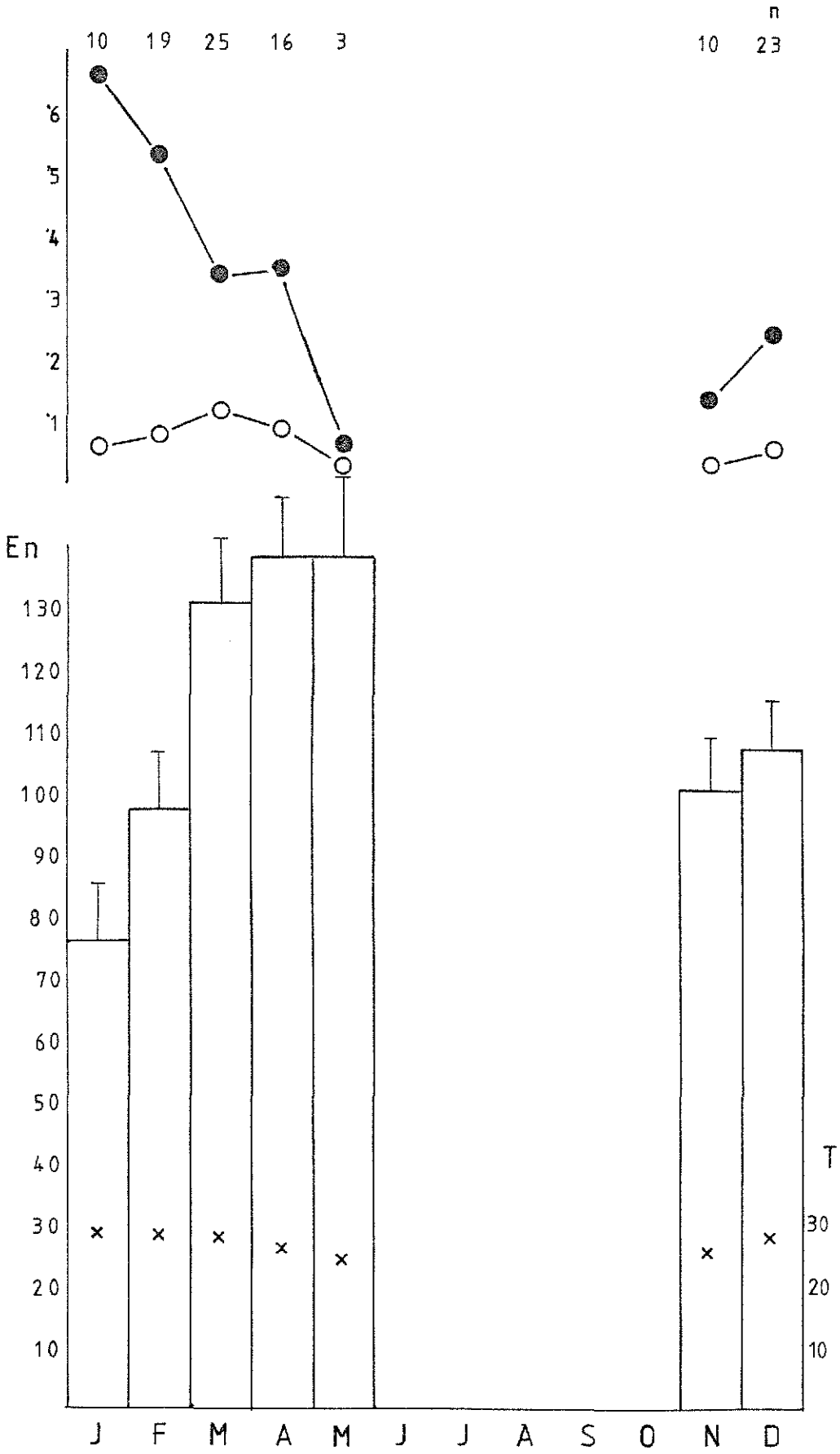
Fig 7b. Mean monthly fecundity and mean proportional inviability and infertility, field-captive specimer Notes as for Fig 7a.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Section 7.4. Discussion

Fecundity and fertility in T. rufipes are independent of temperature, within the range 20-30° C in the laboratory, or at temperatures normally experienced in the field. Specimens were not subjected to lethal or highly stressful temperatures, so the presumed effects of such temperatures on reproductive effort remain unknown. The experimental temperatures quite closely reflect the normal range of mean monthly temperature in the field in this district (19.4-28.0° C), but of course the diurnal temperature cycle was not simulated.

It is unfortunate that temperatures inside the field confinement tubes were not recorded, because it seems highly likely that the abnormally high infertility rate and low fecundities for what are the hottest months of the year arose because the confined specimens had no relief from the combination of heat and high humidity, whereas their free counterparts were afforded some such relief by the movement of air by breezes and/or fans.

While the temperatures experienced by T. rufipes in nature range over 30° C, the range over which normal development was assured seemed closer to 10° C. At a temperature of 20° C few eggs developed normally (see section 7.2), while 30° C may be close to an upper limit of temperature tolerance, as it is for L. hasselti (Downes 1986). Certainly, these and more extreme temperatures can be tolerated for limited periods of time; sacs constructed

at 20° C, for example, were, after exposure to this temperature for the first 1-3 days, routinely transferred to 25° C and suffered no ill effects. Adults are evidently more tolerant of sustained nonoptimal temperatures than are developing embryos and postembryos.

Other results of this study show that most of the total variance observed in fecundity and fertility levels in T. rufipes is explainable by individual differences and by food intake. It is for this reason that correlations of the data were made with respect to rainfall, both directly and for the previous month's rainfall, which may affect insect abundance and hence food availability. No effect of rainfall was detected, however.

Chapter 8. FEEDING EFFECTS

Section 8.1. Introduction

Three aspects of feeding were investigated and are considered in this chapter. These were food availability (or quantity consumed, i.e. feeding rate), food quality and feeding abstinence prior to oviposition.

The selected feeding rates cannot be compared with the natural feeding frequencies of Theridion rufipes, nor with the usual amounts of food consumed, these being unknown. It is likely that natural feeding of T. rufipes is very opportunistic and that quantities consumed and frequency of feeding vary greatly. The limiting factor is probably overabundance, in that there would be a (variable) maximum food intake and feeding frequency beyond which further prey availability would be ignored.

Food quality could only be investigated by varying the type of prey provided, with a view to assessing whether the reproductive variables of the study were affected as a result of the type of food eaten prior to an oviposition. One of the food types (isopods) was discovered, after its use, to be potentially unsuitable as food for spiders.

Hale (1929) explained the unpalatability of woodlice as due to a viscous fluid secreted by the cutaneous glands. Gorvett (1956) confirmed this as a defensive mechanism against spiders (though not against Dysdera or

wolf spiders) and other predators, and the suitability of woodlice as an experimental food source was reviewed by Cloudesly-Thompson (1980). Their use in the present study supports these previous findings, that woodlice, while not universally rejected, are an unpopular prey among theridiid spiders.

The suitability of insect prey types is almost entirely an area of ignorance (Whitcomb 1978). An example that shows how poor our understanding is of food acceptability and/or suitability is the preference shown by Latrodectus mactans and L. variolus for housefly maggots in the study of McCrone and Levi (1964); housefly maggots were rejected, without exception, on the numerous occasions they were offered to L. hasselti (Downes 1986).

Section 8.2. Materials and methods

The six insect food types used were Drosophila, cockroach early nymphs, Tenebrio (mealworm) larvae, isopods, muscoid flies and small wasps (the last only rarely used, in the early trials of the study). The isopods (woodlice, slaters) were taken readily by some spiders and on some occasions and were ignored by others and on other occasions. The other five food types were uniformly acceptable.

To estimate rates of feeding, ten Drosophila or one individual of the other food types were taken to be equal to one prey equivalent. The size of the non-Drosophila

prey were all approximately 1 cm in length apart from the mealworms which were about 1.5 cm long.

Although food supply could not be rigorously quantified (see Chapter 2), rate of feeding was considered likely to be the most important variable influencing the fecundity and fertility of T. rufipes. Accordingly, two feeding regimes were established for the main experimental trial - MAXIMAL (fed two prey equivalents three times a week) and MINIMAL (fed one prey equivalent twice a week). A third regime, SUBMINIMAL (less than one prey equivalent, by offering smaller size prey where appropriate, once a week) was later included for a limited trial. There were four similar feeding trials done in the early years of the study, two (subsequently designated NORMAL) at a rate of one prey equivalent three times a week, and two at feed rates comparable to MAXIMAL as defined above. These were coded separately for comparison as required. All field specimens or those for which no feeding regime was established were coded as 'feed rate not applicable'. The numbers of females and egg sacs for each feed rate treatment were

MAXIMAL	43 females, 240 egg sacs
NORMAL	14 females, 49 egg sacs
MINIMAL	25 females, 103 egg sacs
SUBMINIMAL	10 females, 14 egg sacs

Water was not provided. Forster (1984) confirmed that providing water is not only unnecessary for rearing Latrodectus but may be detrimental; experience showed that it was also unnecessary for maintaining T. rufipes.

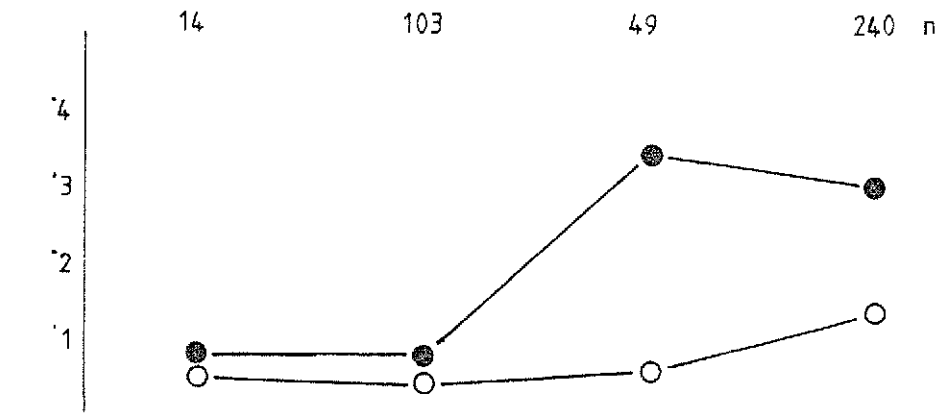
The feeding schedule of experimental laboratory spiders called for feeding at least once a week, so it was only on the occasions that a spider left food untouched for a number of days that data for feeding abstinence up to ten days was obtained; this amounted to relatively few cases, involving only 9 of the 401 egg sacs contributing data to Fig 10.

Section 8.3. Results

Feeding rate influenced both fecundity and fertility (Fig 8), proving highly significant in the analyses of variance results (see Chapter 3) and explaining 19% of the total variance observed in fecundity and 10% of the total variance in inviability.

There were three maximal feed rate trials, done in 1983, 1984 and 1985. The values given for MAX feed rate in Fig 8 is for all three trials combined, the separate means for fecundity of which were 77.3, 119.4 and 134.4. The first of those three values is not consistent with the trend of Fig 8 but it is the mean of only seven egg sacs, from three females. The other two values are the means of 180 and 53 egg sacs respectively.

Fig 8. Mean fecundity and mean proportional inviability and infertility in relation to rate of feeding. Column values (fecundity) supplemented by standard errors. Black dots, INVIABILITY 1 (failure to develop). Open dots, INFERTILITY (undeveloped eggs, full or consumed). SMIN= subminimal, MIN= minimal, NOR= normal, MAX= maximal. En= mean number of eggs per sac. n= number of egg sacs examined.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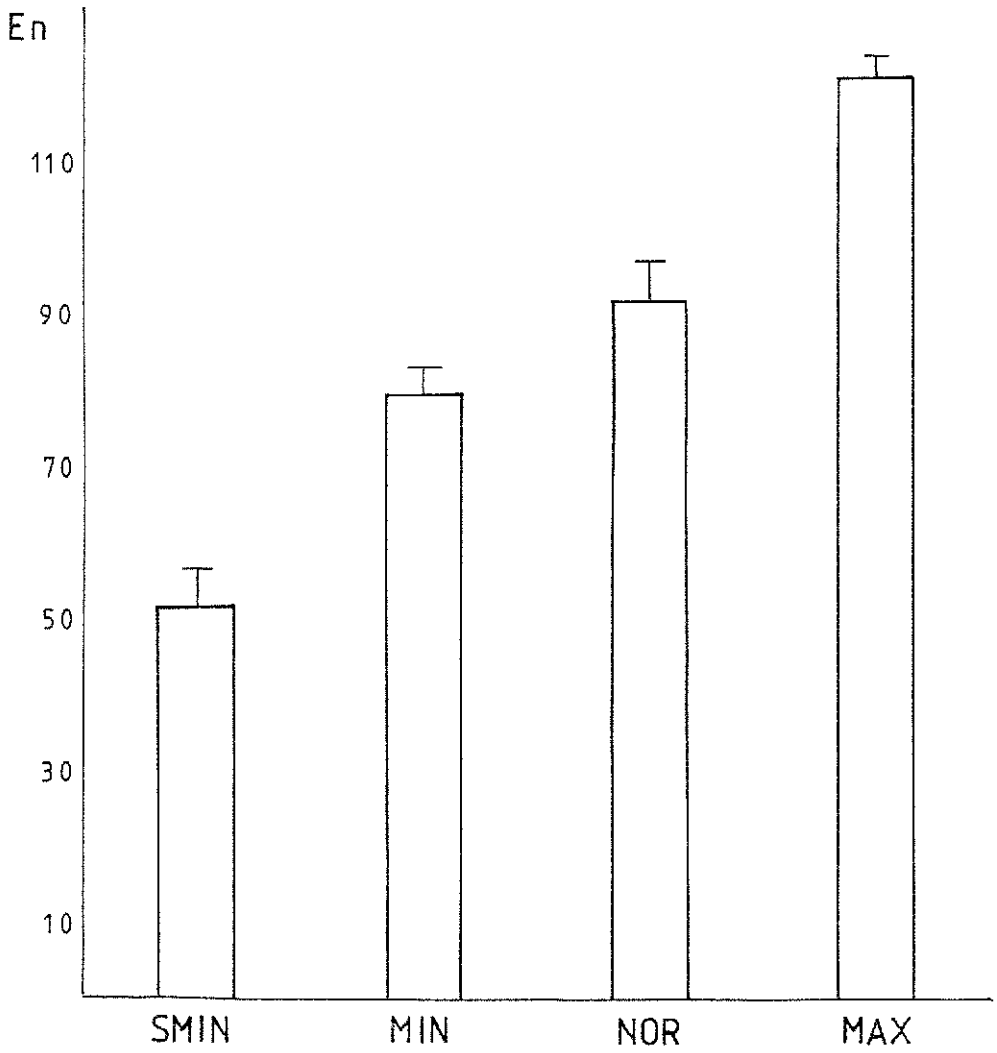
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Fig 9. Mean fecundity and mean proportional inviability and infertility in relation to last food type consumed before oviposition. Column values (fecundity) supplemented by standard errors. Black dots, INVIABILITY 1 (failure to develop). Open dots, INFERTILITY (undeveloped eggs, full or consumed). W= wasp, F= fly, D= Drosophila, M= mealworm, C= cockroach, S= slater. En= mean number of eggs per sac. n= number of egg sacs examined.

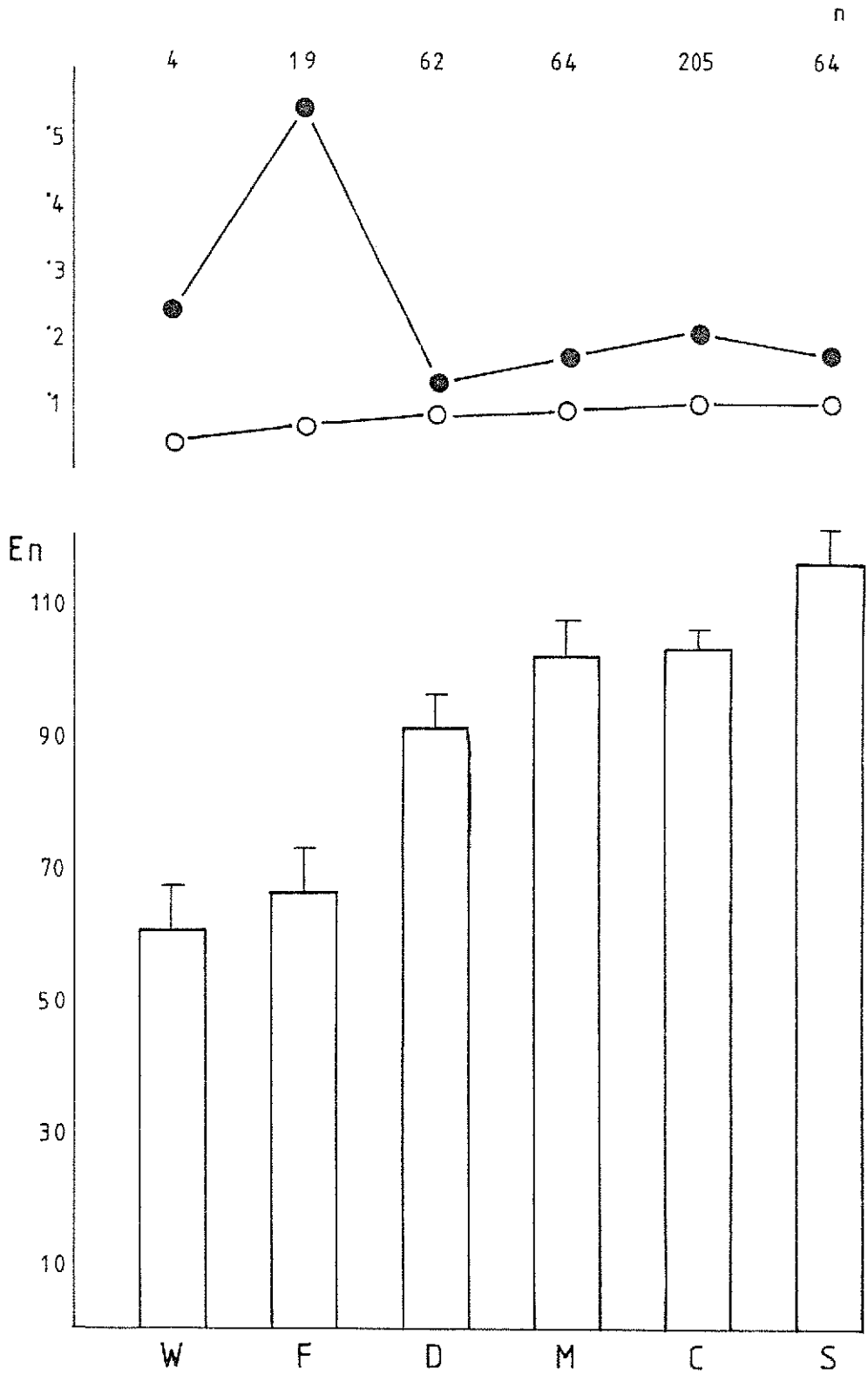
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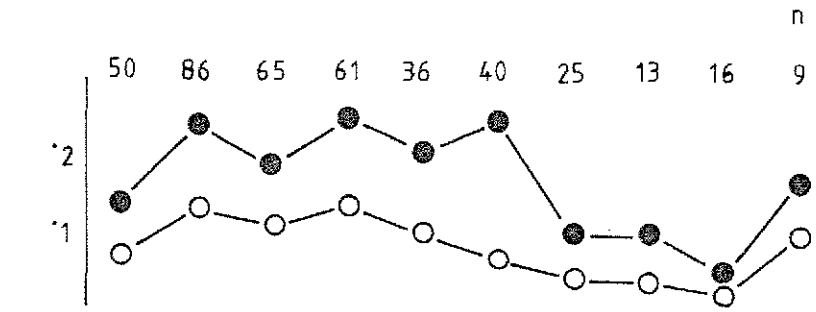
Fig 10. Mean fecundity and mean proportional inviability and infertility in relation to the time elapsed between feeding and ovipositing. Column values (fecundity) supplemented by standard errors. Black dots, INVIABILITY 1 (failure to develop). Open dots, INFERTILITY (undeveloped eggs, full or consumed). En= mean number of eggs per sac. n= number of egg sacs examined.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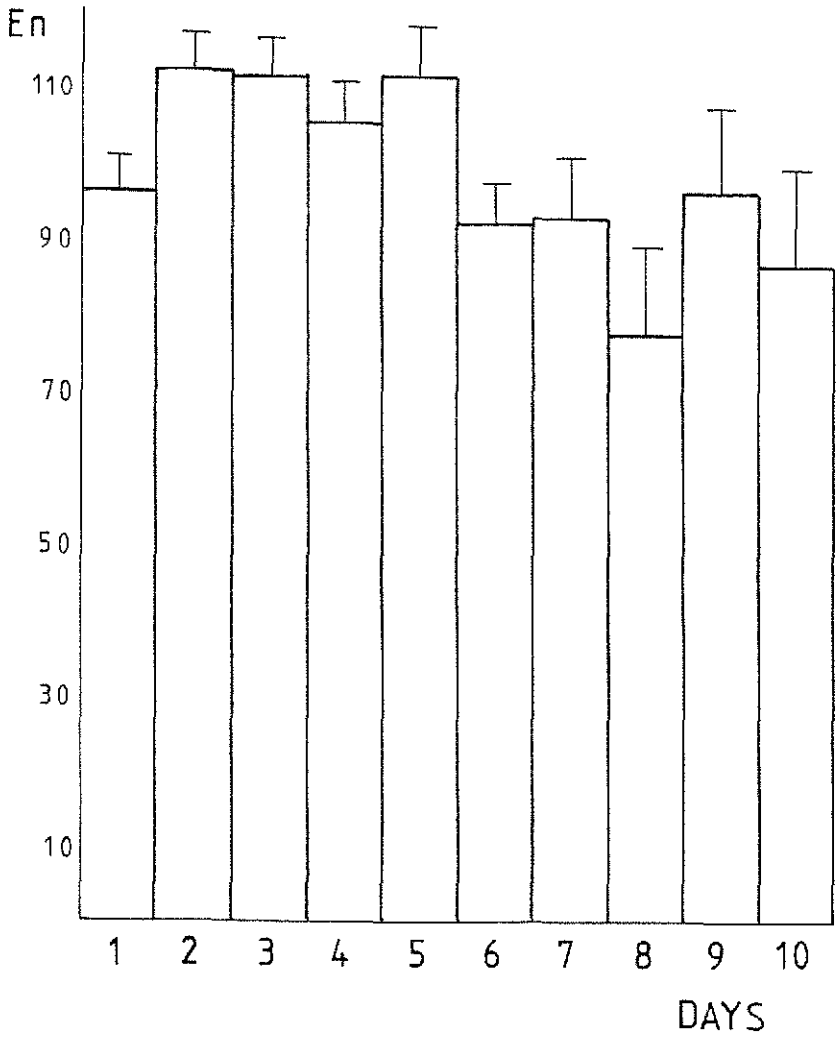
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A rank correlation analysis showed the fecundity relationships of Fig 8 to be significant at the 0.01 level. A test for least significant differences showed that at the 0.05 level only the MINIMAL and NORMAL rates were not significantly different.

Fig 8 expresses the fecundity results in terms of individual egg sacs. Table 6 gives another aspect of the relationship between feed rate and fecundity by expressing the results as a daily productivity rate. The relationship is again significant at the 0.01 level.

Table 6. Mean fecundity expressed as egg productivity per unit time, for three feed rates. Number of egg sacs given in brackets.

Feed rate:	Maximal	Minimal	Subminimal
Mean eggs/day:	9.24 (240)	4.20 (103)	2.20 (14)

Inviability and infertility both increased as rate of feeding increased ($F = 13.5$, $df = 3$, $p < 0.0005$ (Table 2)). Least significant difference tests at the 0.05 level showed that all values of inviability differed and that maximal feedrate infertility differed from the other feedrate values. The impression given in Fig 8, that increasing fecundity leads to increasing infertility could be misleading. Both fecundity and infertility are

responding to the independent variable, feed rate, but not necessarily to each other.

Fig 9 shows the mean fecundity and proportional inviability and infertility for ovipositions following consumption of the six food types. The first food type (wasp) was omitted from the analysis of variance that gave significance levels and computed 4% as the variance contribution of food type to the total observed variance in fecundity (Table 2). When the wasp food type was included, using a one-way ANOVA, the variance contribution value increased to 7%, and the significance levels became 0.0005 (fecundity), < 0.0005 (inviability) and 0.748 (infertility). Least significant difference tests at the 0.05 level showed that woodlice and flies had the most marked effects on the spiders' fecundity, and flies had the greatest effect upon inviability.

The time interval between feeding and ovipositing did not contribute significantly to the total observed variance, either in fecundity or fertility.

In Fig 10, some 75% of the egg sacs were produced within five days of the parent female feeding, and 50% were produced within three days of feeding.

Section 8.4. Discussion

The results of this Chapter show that fecundity and infertility respond positively to rate of feeding. With an increase in feed rate, fecundity increases both in terms

of mean number of eggs per egg sac (Fig 8) and egg productivity per unit time (Table 6). At the highest feed rate, the mean number of eggs per egg sac was more than double, and the mean productivity per unit time more than four times, that at the lowest feed rate.

That fecundity responds strongly to food availability is to be expected. The inverse relationship between feeding rate and fertility was unexpected; a good food supply would be expected to maximize the fertility rate of a female spider, especially if the production of relatively more infertile eggs was a way of enabling spiderlings to live longer, travel farther and thus escape from unfavourable habitats. There may be two explanations for the present results. One is that it is not known where optimal feed rate ends and unnecessary disturbance by overfeeding starts. If excess disturbance lowers 'habitat suitability', increased levels of inviability in egg sacs may result. Alternatively, fecundity and fertility may be functionally unrelated. An examination of the relationship between infertility and fecundity using all 771 egg sacs examined during the study gave a correlation coefficient of -0.052; i.e. there was no correlation between the two. In Chapter 11 and the concluding remarks, evidence will be presented and discussed that the production of inviable eggs by T. rufipes may be better interpreted as fluctuating around an optimum for spiderling dispersal and survival, rather than as a fecundity-linked response to habitat quality.

As stated above, food suitability is an unkown factor, and the results show that it also has an effect on fecundity (Fig 9). The loose nature of the experimental design, and the wide variation in numbers of cases for the various food types used, make the data less definitive than they might otherwise have been, but one remarkable feature stands out: fecundity was at its highest directly after feeding on isopods (slaters), of all the insects used the only type known to be unacceptable to many spider species. Consumption of isopods did not affect the fertility rate in any significant way. The defensive distastefulness of woodlice may have evolved precisely because they are otherwise highly acceptable and suitable as a prey type. From this point of view, the present results are not at all surprising.

Ants, although not used in this study, are very common victims in theridiid webs in Townsville. They constituted 88% of the food of Theridion saxatile in a study by Norgaard (1956).

Fig 10 suggests that egg sacs produced between 2-5 days after feeding tend to be largest, though not the most fertile. The variation is not significant, however.

Chapter 9. LOCALITY AND POPULATION STRUCTURE

Section 9.1. Introduction

The specimens of Theridion rufipes used in this study came from two locations, as described in Chapter 2. Though it was not originally an aim of the investigation, the possibility that reproductive performance might be shown to differ between specimens from the two locations became a point of interest. When differences did become apparent, an account of these results was prepared as a separate chapter and is presented here.

Whether the observed differences are due to the demic structure of T. rufipes populations cannot be decided. Theridiid spider populations are far from panmictic and, for reasons discussed below, this is especially so with T. rufipes, but the breeding structure and patterns of gene flow in theridiid populations are unknown.

Section 9.2. Materials and methods

There are no techniques or procedures relevant to this chapter that have not already been described in Chapter 2.

In the first year of the study, location of origin was not recorded, so of the overall total of 771 egg sacs examined during the study only 707 make up the data set for this chapter.

Section 9.3. Results

The source location (ORIGIN) of specimens was included in the analysis of variance (Table 2) that was outlined in Chapter 3. This showed that ORIGIN explained only 2% of the total observed variance in inviability and 5% of the variance in infertility, but that it did have significant effects in each case.

A comparable ANOVA in which only those specimens collected in 1985 were included in the data for ORIGIN gave similar significance levels (inviability, p= 0.015, infertility, p= 0.001). ORIGIN contributed 1% of the total observed variance in each case. Fecundity also proved to differ between the two groups in 1985, contributing 1% of the total observed variance and having a significance level of 0.064.

The above analyses separated out the effects of feeding rate, food type and the sac sequence; the large residual variance was almost entirely due to individual differences; the egg sacs produced by individual females tended to be relatively homogeneous.

Fig 11 shows graphically the mean fecundity and fertility of the egg sacs from the two subpopulations of T. rufipes. It demonstrates that individuals from the Cranbrook subpopulation exhibited lower fecundity in 1985 while showing no such difference over the study period as a whole. To a varying extent, inviability and infertility

are lower in the Cranbrook subpopulation in both cases.

Section 9.4. Discussion

The two subpopulations may be relatively isolated. The Cranbrook house, for example, was partially flyscreened, and while insect prey in great abundance actively found entrance to the house, passively dispersing spiderlings from other areas were far less likely to enter. The subpopulation within the house could not therefore be considered panmictic with other local T. rufipes subpopulations. On the contrary, there was good reason to consider it a little inbred. Similarly, the subpopulation of T. rufipes from the James Cook University campus, or at least that part of it that inhabited the enclosed stairwells of the Biological Sciences building, may have very little immigration from other areas. The various comparable subpopulations inhabiting suitable sites may therefore comprise a pattern of relatively isolated demes.

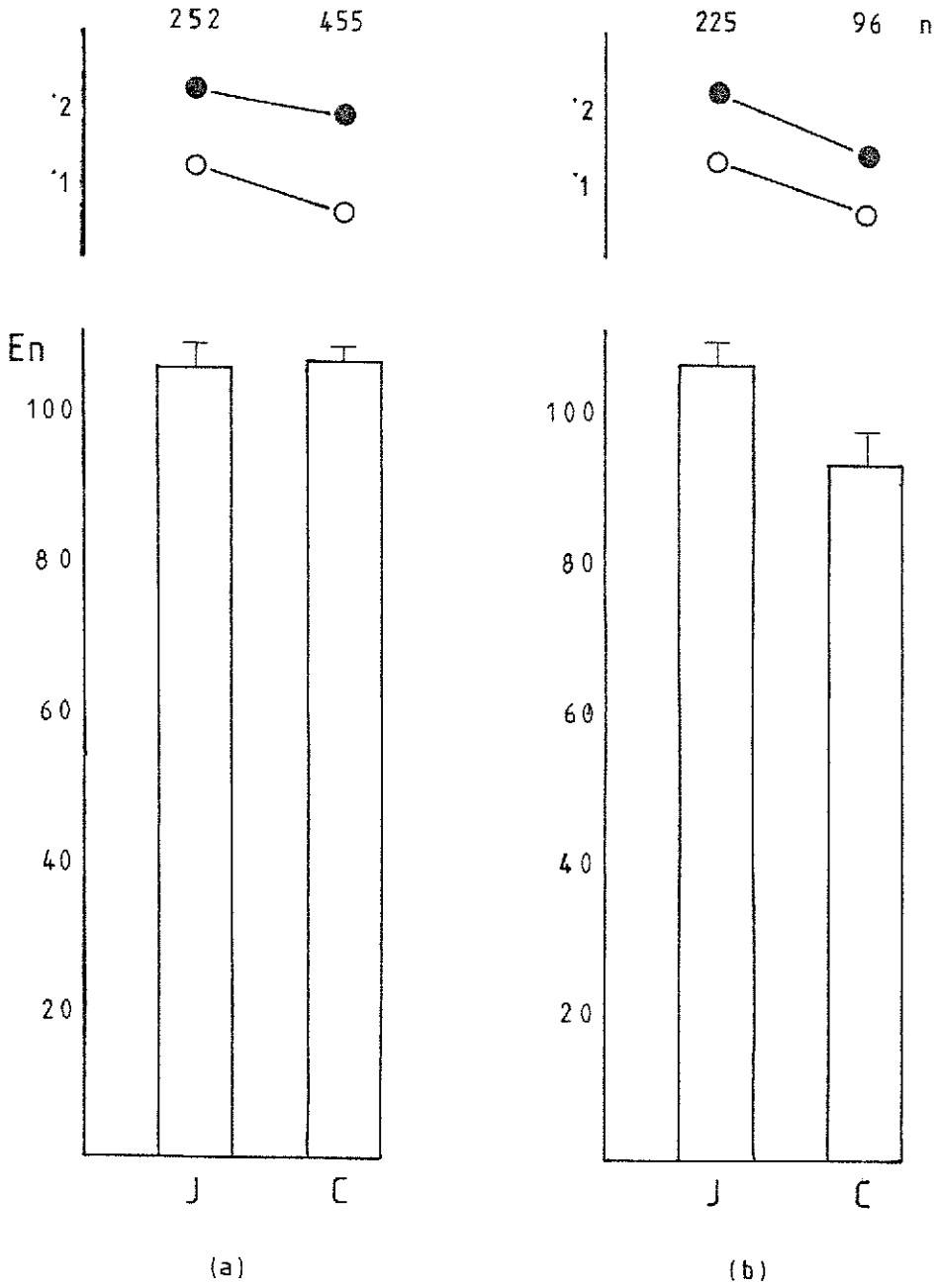
Whether observed differences between the two groups reflect different environmental history, genetic variation, or both, cannot be determined from the available data.

If, as the results suggest, the spiders of the James Cook University campus tend to produce a higher proportion of inviable and/or infertile eggs than do the spiders of Cranbrook origin, there are two possible reasons for it.

1. The Biological Sciences building is treated internally and externally for pest control on an annual basis. This temporarily reduces the spider population and has unknown residual effects. No such commercial pesticides have been used in or around the Cranbrook location during the time of this study. That the University campus population is no less fecund than the Cranbrook population suggests that this factor does not have any long-term suppressive effect on the spiders.

2. T. rufipes, living as it does almost exclusively in the enclosed areas of buildings, depends to a large extent on artificial lighting at night which attracts insect prey. Variation in the regularity and duration of lighting between the two locations may influence food availability, which has been shown to influence fertility. Since the data used was from spiders kept in controlled conditions, this explanation, if correct, would imply that feeding regime has long-term as well as short-term effects; e.g. better food availability as a juvenile may result in differential fertility as an adult.

Fig 11. Mean fecundity and mean proportional inviability and infertility of subpopulations (demes), (a) between 1980-85 and (b) in 1985. Column values (fecundity) supplemented by standard errors. Black dots, INVIABILITY 1 (failure to develop). Open dots, INFERTILITY (undeveloped eggs, full or consumed). J= James Cook University campus specimens. C= Cranbrook specimens. En= mean number of eggs per sac. n= number of egg sacs examined.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Chapter 10. DISTURBANCE AND CONFINEMENT

Section 10.1. Introduction

Among the variables routinely recorded on the data sheets for the study were VIALOVIP (the time between changing the vial of a subject female, to keep the vial clean, and the next oviposition) and MATEFORL (a code indicating whether the female concerned had mated in the field or in the laboratory). These variables were potentially useful indices of disturbance and confinement respectively. One further indication of the effects of confinement would be a difference in fecundity and/or fertility between egg sacs constructed in the laboratory and in the field. These effects are considered in this chapter.

In several places above, the unknown extent and effects of disturbance and confinement have been acknowledged, and it has been stated previously that results of laboratory studies are unavoidably influenced by these factors (Downes 1986), although their effects can and should be minimized.

Section 10.2. Materials and methods

A total of 182 egg sacs were constructed in the laboratory within ten days of a vial change. Those constructed on even numbers of days after such a change

were selected to check for any regularities or trends.

Because female T. rufipes specimens typically occupy the underside of container lids when they are confined, a vial change can usually be effected rapidly by removing spider and lid together and replacing these atop a fresh vial. This procedure does however tear the web which normally extends to the base of the vial, and occasionally a spider would drop to the bottom of the vial before the lid was fully removed. The disturbance of the vial change therefore varied in its extent.

A value for VIALOVIP was not entered on a data sheet for a given egg sac if there was no change of vial between the oviposition date of that sac and the previous oviposition. In the case of first ovipositions, the date of original confinement of the specimen was taken to be equivalent to a change of vial, if no vial change had occurred between the confinement date and the first oviposition.

There were 173 known field-mated females, and these produced 479 of the egg sacs examined during the study. There were 56 known laboratory-mated females and these produced 256 sacs.

Section 10.3. Results

Fecundity and fertility did not alter with respect to the number of days elapsed between a vial change and oviposition (Fig 12). The variable VIALOPVIP contributed

nothing to the total observed variance.

There were also no significant differences in mean values for fecundity or fertility according to whether the female mated in the field or the laboratory (Fig 13). A relatively large number (735) of egg sacs served as the database in this case. Analysis of variance gave similar results for MATEFORL as it did for VIALOVIP.

Differences in fecundity and inviability did arise between egg sacs produced in the field and those produced in confinement (Table 7). The laboratory sacs were, at the 0.05 level, significantly less fecund and more viable than the field sacs.

Table 7. Overall mean fecundity and mean proportional inviability of laboratory and field egg sacs. Standard errors in brackets.

	n	fecundity	inviability
Lab	456	101.8 (1.96)	0.17 (0.012)
Field	311	112.4 (2.45)	0.23 (0.017)

Section 10.4. Discussion

Apart from the confinement itself, there were three main components of disturbance - feeding, changing vials and removing egg sacs. Surprisingly, the results of Fig 12 do not show that longer periods without disturbance resulted in any change in fecundity or fertility. The

simultaneous influence of the other two components of disturbance would have modified any disturbance effect that may otherwise have existed independently of them, but, if the VIALOVIP results cannot be taken as conclusive they can at least be taken to indicate that if that disturbance component has an effect it is not a large one.

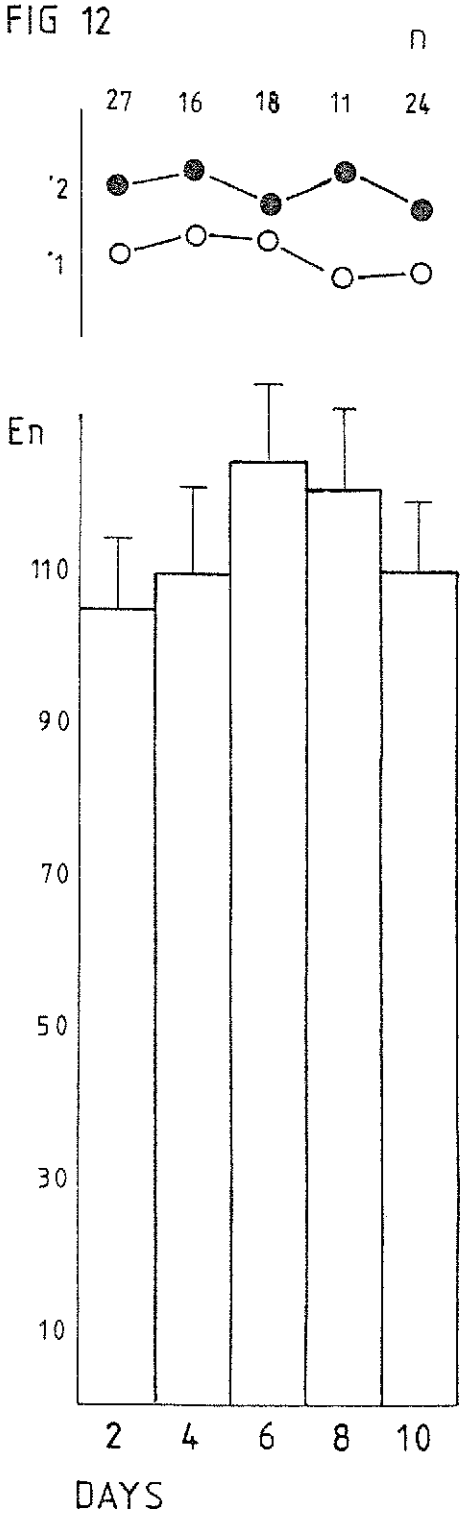
This suggests that confinement per se probably does not produce unrepresentative or misleading results. Similarly, Fig 13 indicates that mating in an artificial environment certainly did not have any effect on fecundity and fertility.

These results permit a slightly more informed interpretation of the differences apparent between laboratory and field-produced egg sacs (Table 7), inasmuch as the differences are probably not due to confinement as such. Bouillon (1957b) found fewer empty chorions in field-collected egg sacs of Latrodectus geometricus; this contrasts with the present results for T. rufipes if number of empty chorions is taken as implying that proportional infertility and/or inviability was higher.

Fig 12. (LEFT) Mean fecundity and mean proportional inviability and infertility in relation to the time elapsed since a vial change. Column values (fecundity) supplemented by standard errors. Black dots, INVIABILITY 1 (failure to develop). Open dots, INFERTILITY (undeveloped eggs, full or consumed). En= mean number of eggs per sac. n= number of egg sacs examined.

Fig 13. (RIGHT) Mean fecundity and mean proportional inviability and infertility in relation to location of mating. F= field. L= laboratory. Other notes as for Fig 12.

FIG 12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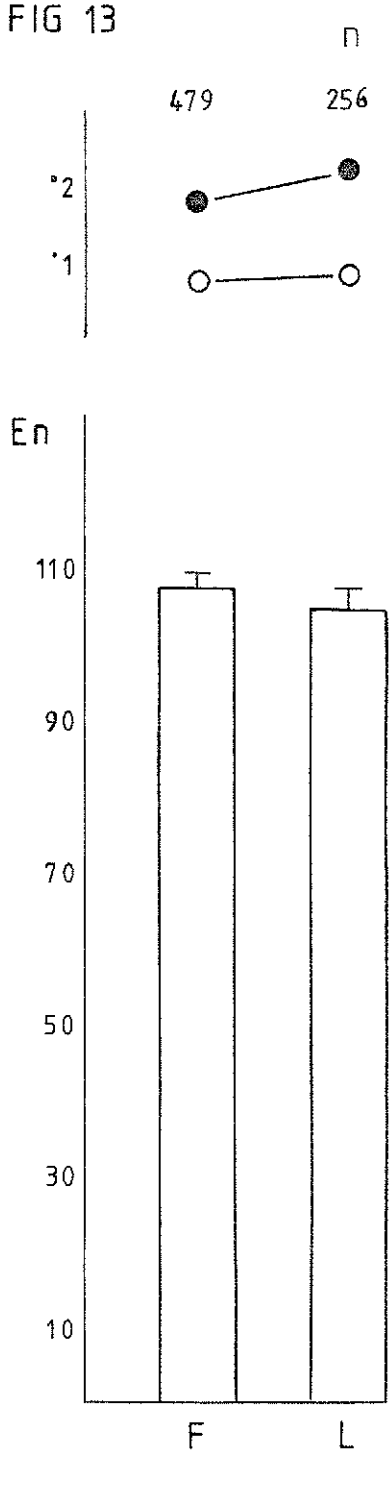
DAYS

FIG 13


n
479
256
°2
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Chapter 11. SURVIVAL - THE DIVIDEND

Section 11.1. Introduction

That the consumption of undeveloped eggs by first instar spiderlings improved their prospects of survival was a hypothesis that, despite evidence from previous authors (Schick 1972, Valerio 1974), had to be tested for the present study. All that was possible was to determine what growth and survival enhancement occurred as a result of oophagy. This chapter reports these findings, and in doing so is able to include data on the relationship between quantity of egg material eaten and probability of molting to third instar without further food intake. This latter aspect of the question complicates the otherwise straightforward notion that the bigger the prefeed the longer the spiderling will probably resist starvation.

The egg-feeding behaviour of T. rufipes spiderlings takes place within a protective cocoon which may contain from just a few to several hundred eggs. The many types of spider cocoons and ideas on their numerous functions will not be considered here, but it is well to note that it is nearly always an active, 'complete', self-sufficient spiderling that emerges from the cocoon. Exceptions to this include wolf spiders and some spider species (e.g. Polybetes (Galiano 1971)) in which the parent opens the cocoon to allow the spiderlings, which still depend on yolk reserves, to come and go from it. An understanding of

previous developmental events is essential to an appreciation of what stage of development the emergent spiderling has reached, what to call it and why, and (the central theme of this thesis) in what ways previous events have influenced its potential for growth, dispersal and success.

Most theridiid and many other spiderlings disperse on the wind (anemochory) and the distances travelled in this way may be minute or enormous. Given appropriate atmospheric conditions, dispersing spiders may ascend to heights of 5000 metres (Glick 1939) and be passively transported in the 'aerial plankton' over prodigious distances (Bristowe 1930). How long such journeys take is unknown, but it can fairly be assumed that an ability to withstand starvation for a period of days, weeks or longer is a desirable attribute for spiderlings that may not only have to undertake an unexpectedly long atmospheric odyssey but will, just like those that disperse only as far as the adjacent outhouse, have to find a suitable web site, establish a web and await their first prey.

Simple isolation of emergent spiderlings enables the potential duration of survival without food to be determined. In the context of the present study, it also should show the effects, if any, of prior consumption of unecloded eggs where this has occurred.

Section 11.2. Materials and methods

To determine the survival potential of spiderlings after emergence from the egg sac, whole broods of emergent spiderlings were segregated individually into glass tubes 50 mm x 10 mm lightly plugged with non-absorbent cotton wool (Plate 2a). Any living spiderlings that remained within an egg sac after the whole emergent brood had been segregated were also separated into glass tubes in the same way; any that were malformed or stuck within the egg sac (see Chapter 2) and which died before any deaths had occurred among the normal brood were considered abnormal for purposes of survival testing and were excluded from the analysis.

The tubes were kept at 25° C and checked daily, records being kept of deaths and of molts to second instar where these occurred.

A total of 23 broods were treated in this way. For each brood, apart from the infertility formulae routinely computed, a new variable, EGGEQUIV (mean number of egg equivalents consumed per spiderling) was computed. There were two alternative formulations for this variable:

1. Empty chorions / Number of viable first instar spiderlings.

2. (Empty chorions + (0.5 * Half-empty or partly-collapsed eggs)) / Number of viable first instar spiderlings.

The second assumes that none of the eggs collapsed and degenerated without having been fed upon to some extent by the spiderlings. These two formulae enabled longevity of broods and of individuals to be correlated with the mean amounts of egg food material consumed.

To avoid confusion it should be noted here that the longevity or starvation resistance time of second instar spiderlings is taken as commencing at emergence from the egg sac. To say, then, that a first instar spiderling lived for 50 days and a second instar spiderling lived for 60 days is to say that the latter lived ten days longer than the former, both times taken from emergence; it does not mean that the second instar spiderling lived for 60 days over and above its time spent as first instar.

Section 11.3. Results

Egg-feeding increased both the probability of molting and the longevity of starved spiderlings.

Table 8 lists the two different formulations of EGGEQUIV (mean number of egg equivalents consumed per spiderling), computed as described above, but only the first formulation is used in Figs 14a-f. All except two of the corresponding values of the two formulations are very similar, most of them almost identical; there is therefore nothing to be gained by presenting both formulations graphically.

Egg sac 9/1 (first row of Table 8), which had the highest EGGEQUIV value and whose spiderlings could have been expected to molt without exception, left a single unmolted individual, possibly as a result of a conspiracy to confound the data but more likely because the spiderling concerned did not for some reason eat as much as its fellows did, or perhaps was in some way defective. The data suggest that it must have eaten some egg material, but since it did not molt it adds an outlying data point.

Fig 14 comprises six graphs. The first two (14a and 14b) show the mean and maximum starvation resistance time, respectively, for first instar spiderlings with respect to the number of egg equivalents consumed. Each of these graphs has 22 plotted points, since in one of the 23 broods listed in Table 8 all individuals molted. Notwithstanding the single outlying point, each graph shows a gradual increase in starvation resistance time with an increase in egg material consumed. From Figs 14a and 14b it can be seen that no individuals other than the possibly defective one of sac 9/1 remained as first instars after consuming 0.6 egg equivalents or more. The molt therefore sets an upper limit of about 80 days to the longevity of first instar spiderlings (Fig 14b).

The third graph (Fig 14c) depicts the probability of molting to second instar for first instar spiderlings consuming various quantities of egg material. Some egg-feeding would appear necessary for molting, but as little

as 0.1 egg equivalents may be sufficient. However, it must be recalled that the plotted values are means for given broods and that the actual distribution of the egg food resource would not have been an even one. Some individuals would have consumed more than the mean value, some less, and it is likely that the former spiderlings were the ones that molted. Molting becomes highly probable above 0.8, and virtually certain above 1.2, egg equivalents. In Fig 14c the molt probability for an egg equivalent value of 2.26 is less than 1.0 because this brood (sac 9/1) included the suspect individual that did not molt.

Figs 14d-f show respectively the minimum, mean and maximum starvation resistance times for second instar spiderlings. Eight broods (columns 2/F, 2/M and 2/L of Table 8) are represented. Seven plot points appear in Figs 14e and 14f because in each case one of the plot points is identical for two of the broods (see Table 8). Since no molts occurred without at least some food intake, no values corresponding to zero egg equivalents appear on these three graphs. Each shows the same pattern of response to increasing amounts of egg food consumed, i.e. an initial increase in starvation resistance time of about 20 days between 0.1 and 0.3 egg equivalents, with no continued increase at higher levels of food intake. The values plotted are brood means, however, and very likely underestimate egg material consumption, as explained above.

A comparison of Fig 14b with Fig 14f shows that, for

comparable amounts of egg food consumed, molting did not enhance the prospects of longevity under starvation.

Section 11.4. Discussion

A spiderling's energy budget inflates dramatically (by as much as an order of magnitude in Argiope aurantia and Mecynogea lemniscata (Anderson 1978)) after emergence as a result of a marked increase in activity. Latrodectus tredecimguttatus spiderlings may overwinter without food for months in their cocoons but die relatively quickly after emergence (Shulov 1940). Even without this consideration, the newly-emerged spiderlings are more likely to starve than any later instars because they have to find a suitable web site and establish their webs before they can hope fo feed (older spiders sometimes change web sites but this does not invalidate the latter statement).

Food intake prior to emergence, by consuming unecloded eggs, not only gives the emergent spiderlings a better chance of becoming established but may quite often enable them to molt to the next instar, hence attaining larger size and thus extending their prey range, without additional food intake (Schick 1972, Valerio 1974, this thesis).

Water intake extends the absolute starvation resistance time of emerged first instar Misumenops spiderlings, but not the relative survival time of those

that had and had not fed upon eggs prior to emergence (Schick 1972).

The results given in this Chapter show the extent of the benefits of egg-feeding, which increase progressively with the consumption of amounts between 0.1 and 0.6 egg equivalents. There are much greater proportional increases in starvation resistance times than Schick (1972) reported for Misumenops.

Four of the means in table 8 involved egg sacs of 100% fertility (six of the ten broods listed with 0.0 egg equivalents had minute proportions of inviable eggs) and there was therefore no prefeeding in these cases by the spiderlings. A mean starvation resistance time of 19.5 days is computed for these spiderlings; this value can be taken as the mean baseline for dispersal, habitat selection, web construction and the first successful capture of prey. A prefasted spiderling may not, however, have this full time available for these activities. Observations on the spiderlings starved during this experiment suggested that between 4 and 10 days before dying they had become too weak to set a web and subdue prey.

Those spiderlings that obtain some extra nourishment from unecloded eggs but remain in their first instar are not necessarily at a disadvantage compared to those that molt to second instar without further food intake. Certainly the mean starvation resistance period is greater for those individuals that have molted than it is for

those that have not; but this is more a reflection of the relatively large quantities of egg material that the former have consumed, not an indication of the benefits of molting. The results show that in broods where some spiderlings have molted and some have not the last individual to succumb to starvation was, with but a single exception, a first instar spiderling. The reason for this is that the molt itself consumes energy reserves that are conserved by those individuals that remain as first instars. If, then, first instar spiderlings consume an amount of egg material just short of what would probably induce a molt, they may survive as long as 77 days before starving. This would enable them to travel great distances were they swept up into the 'aerial plankton', though whether and to what extent they could resist the low temperatures of elevations above 2-3000 metres is an unknown question.

Egg material is good travelling food for ballooning spiders. Spider eggs, like most other eggs, have a high lipid content, which not only provides double the energy per unit mass as does carbohydrate and protein but affords twice as much water on oxidation, to the special advantage of small organisms travelling in the air (Anderson 1978).

The 'critical' amount of egg material above which molting becomes more likely than not appears from Fig 14c to be about 0.4 egg equivalents. At a consumption rate of more than 0.8 egg equivalents molting becomes highly probable and it seems, notwithstanding aberrant

individuals like the one encountered in egg sac 9/1, that a food intake greater than about 1.2 egg equivalents ensures that the feeder will molt. As seen in table 8, the highest value for mean egg equivalents consumed per spiderling was 2.26/2.70 which, unless each of the 26 spiderlings concerned ate exactly the same amount, means that spiderlings are capable of consuming more than that.

Second instar theridiid spiderlings can appear within a day or two of emergence, or even before emergence. Kaston (1970) reported instances of heavily prefed third and later instar individuals of Latrodectus still inside unbreached egg sacs, and this phenomenon was encountered in T. rufipes and L. hasselti during the time of the present study.

When molts occurred among the starved spiderlings of this study, they did so relatively early in the starvation period. The mean time lapse from emergence to molting was 9 days and the longest recorded period was 18 days. This contrasts with Valerio's (1974) account of starved Achaearanea tepidariorum spiderlings molting to second instar on the 30th day.

Of those spiderlings that did in fact molt to second instar, most survived more than double the mean starvation resistance time of unfed first instar spiderlings. The mean resistance time for molted spiderlings was 49.5 days, well in excess of double the mean for unfed, unmolted spiderlings. The maximum starvation resistance time was, as noted above, in only one case greater than for prefed

first instars. This involved an individual which may have consumed something like three egg equivalents and which lived for 87 days. It must not be forgotten that increase in body size, and hence access to a different and possibly wider spectrum of prey, is an added advantage of molting that may well compensate for the energy investment of the second ecdysis.

Table 8. Survival time and prefed molting in starved spiderlings. Data for 23 broods.

EE1	EE2	n	1/F	1/M	1/L	PM	E1/F	E1/M	E1/L	2/F	2/M	2/L	CM
2.3	2.7	27	52	52	52	.96	6	11	13	43	61	87	61
0.0	0.0	48	12	16	21	0							16
0.0	0.0	107	15	18	22	0							18
1.3	1.8	15	-	-	-	1.0	7	8	11	34	56	67	56
0.1	0.1	156	19	32	59	.12	8	10	17	31	41	49	33
0.1	0.2	102	5	27	55	.08	8	9	18	38	41	49	28
0.0	0.1	109	14	28	52	0							28
0.0	0.0	121	18	25	47	0							25
0.1	0.3	79	27	38	61	.03	10	10	11	41	43	44	37
0.0	0.0	50	16	20	36	0							20
0.2	0.2	101	28	35	68	.07	9	9	10	42	47	51	35
0.3	0.8	25	29	43	66	0							43
0.2	0.2	42	21	41	77	.21	5	7	9	44	53	60	43
0.5	2.3	13	37	53	74	.69	8	8	12	50	54	65	53
0.0	0.0	118	15	24	45	0							24
0.0	0.0	137	20	25	51	0							25
0.0	0.0	158	13	26	49	0							26
0.1	0.1	111	17	27	54	0							27
0.1	0.1	72	24	27	54	0							27
0.0	0.1	94	11	21	48	0							21
0.0	0.0	46	21	24	32	0							24
0.0	0.0	153	12	26	37	0							26
0.0	0.0	49	20	27	56	0							27

Legend for Table 8:

EE1	Egg equivalents, formula 1
EE2	Egg equivalents, formula 2
n	Number of living first instars on emergence
1/F	Number of days to first death (first instars)
1/M	Mean number of days survived by first instars
1/L	Number of days to last death (first instars)
PM	Probability of molting
E1/F	Number of days from emergence to the first occurrence of a molt
E1/M	Mean number of days between emergence and molting, for those individuals that molted
E1/L	Number of days from emergence to the last occurrence of a molt
2/F	Number of days to first death (second instars)
2/M	Mean number of days survived by second instars
2/L	Number of days to last death (second instars)
CM	Combined (i.e. first and second instars) mean number of days to death

Note that the first listed brood in Table 8 is that of brood 9/1, which contained a possibly defective individual.

Fig 14. Post-emergence starvation resistance and molting probability, in relation to amount of egg material consumed prior to emergence. Note that all resistance times are taken as commencing from emergence (see section 11.2).

Fig 14a. Mean resistance time, first instar spiderlings. Each plotted value is the mean for a single brood (i.e. the progeny of a single egg sac). EE= egg equivalents (see section 11.2).

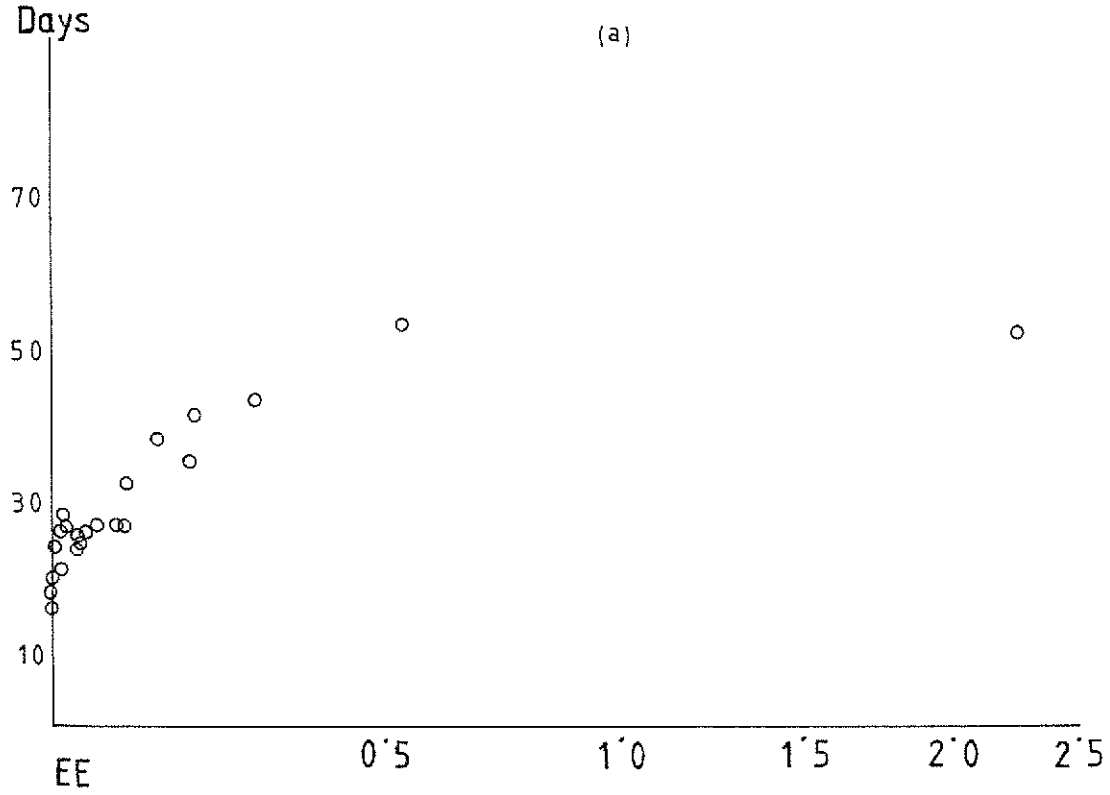

Days
(a)
70
50
30
10
EE
0·5
1·0
1·5
2·0
2·5

Fig 14b. Maximum resistance time, first instar spiderlings. Notes as for Fig. 14a.

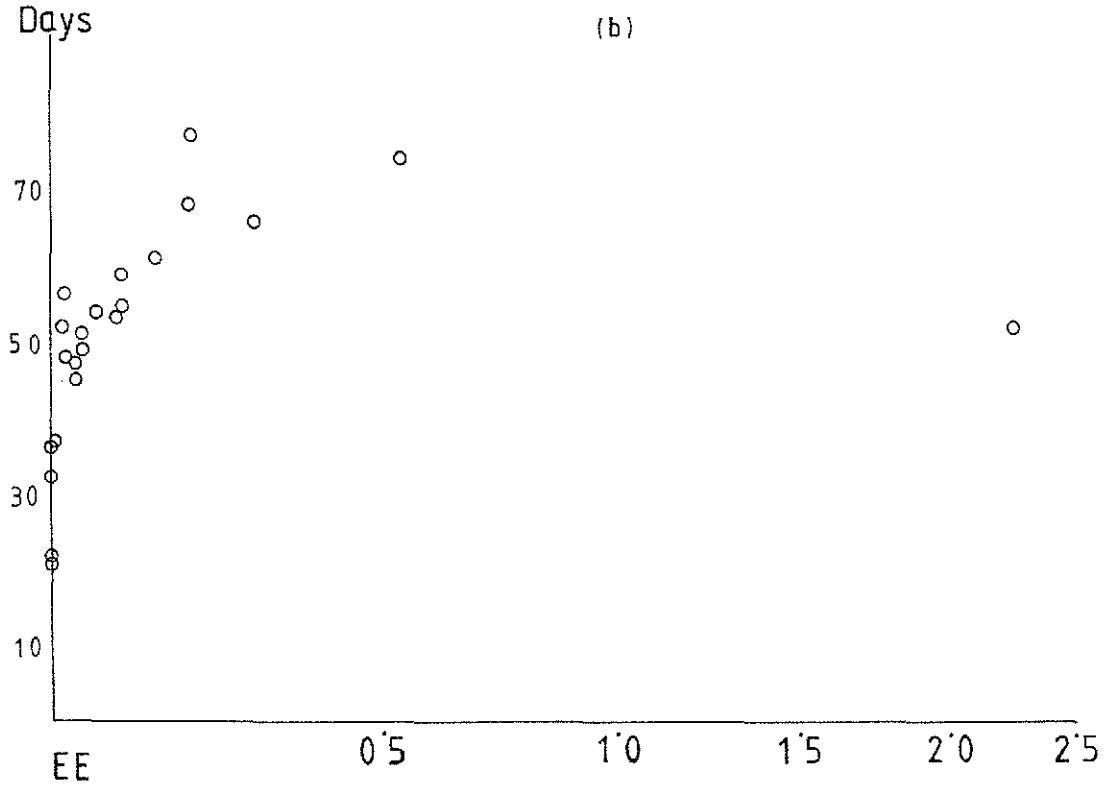

Days
(b)
70
50
30
10
EE
0·5
1·0
1·5
2·0
2·5

Fig 14c. Probability of molting to second instar. MP= molting probability. Other notes as for Fig 14a.

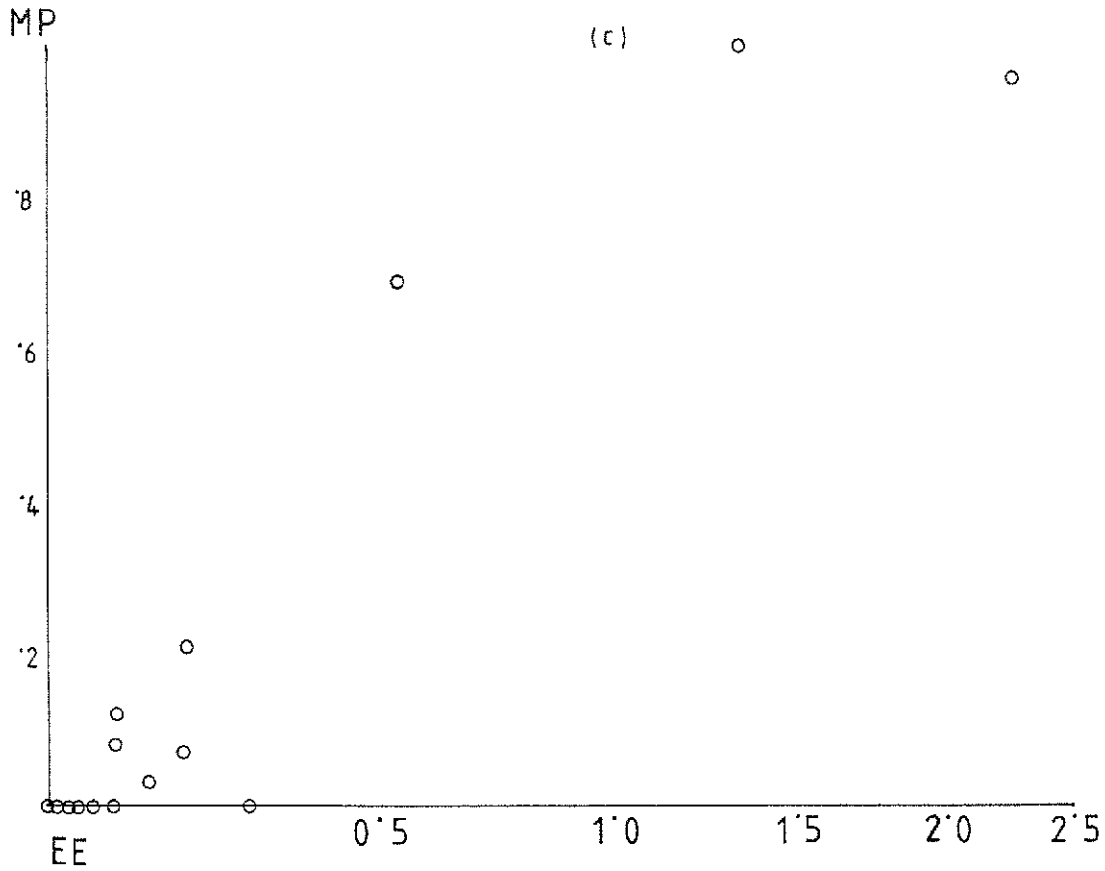

MP
(c)
·8
·6
·4
·2
EE
0·5
1·0
1·5
2·0
2·5

Fig 14d. Minimum resistance time, second instar spiderlings. Notes as for Fig 14a.

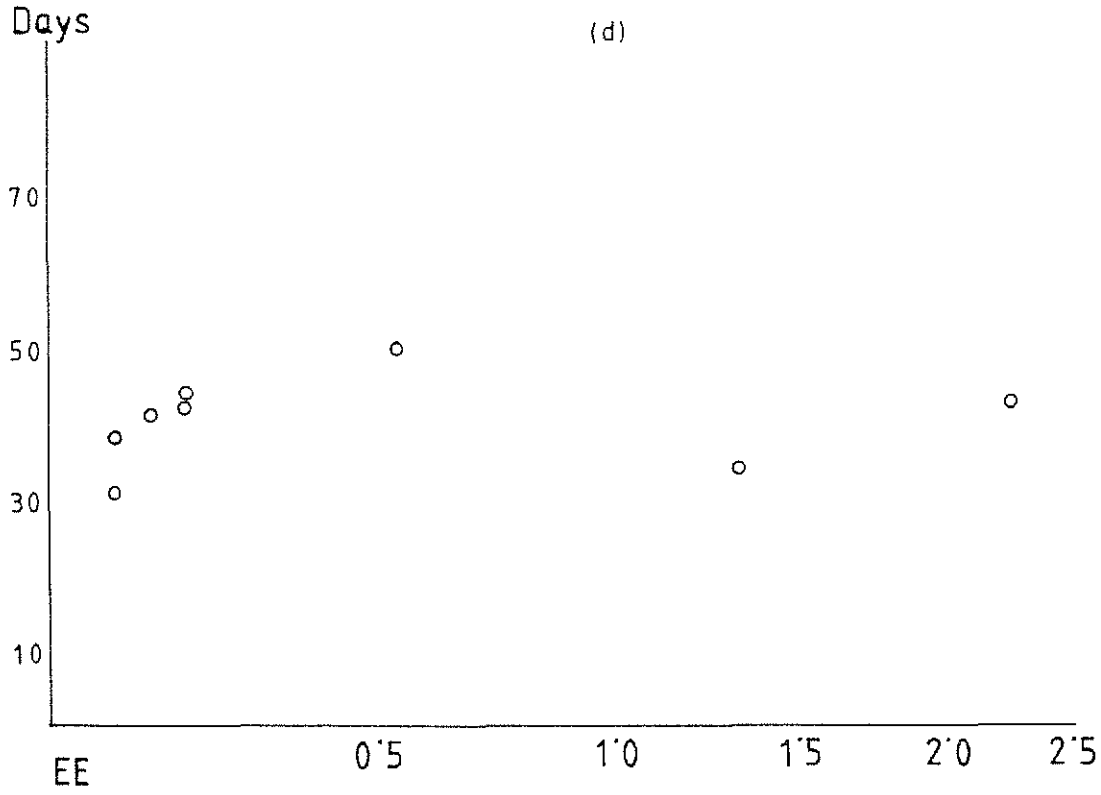

Days
(d)
70
50
30
10
EE
0·5
1·0
1·5
2·0
2·5

Fig 14e. Mean resistance time, second instar spiderlings. Notes as for Fig 14a.

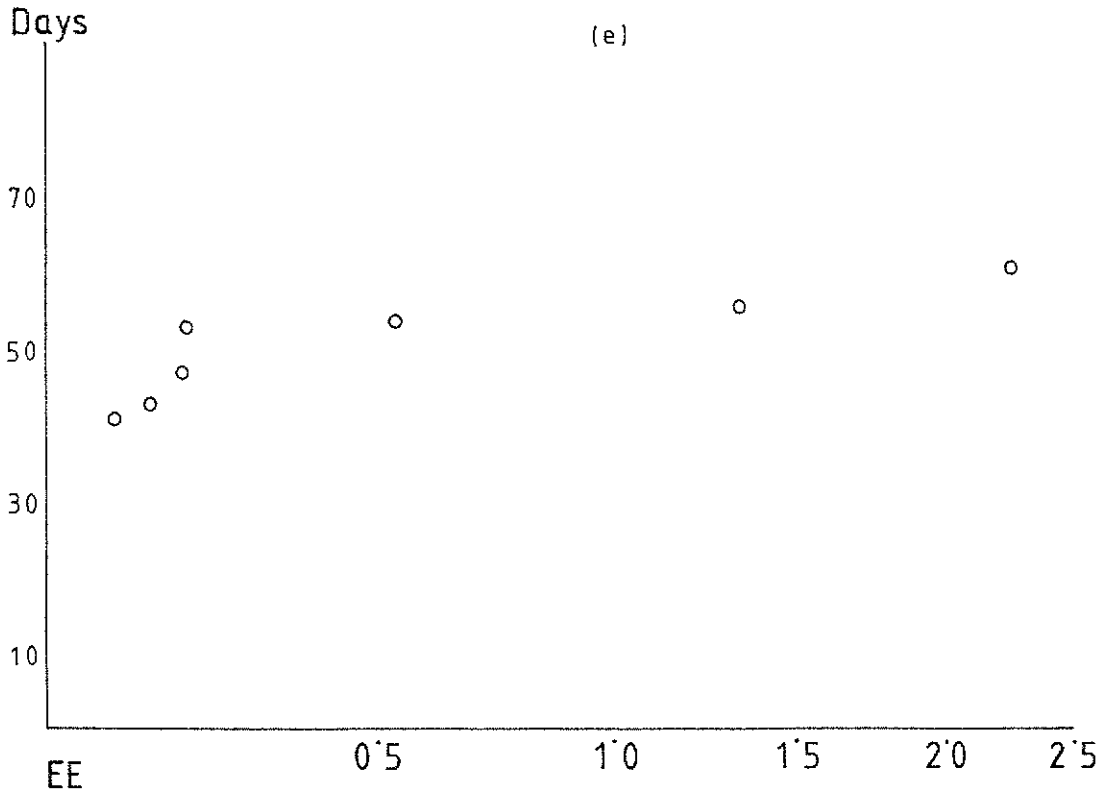
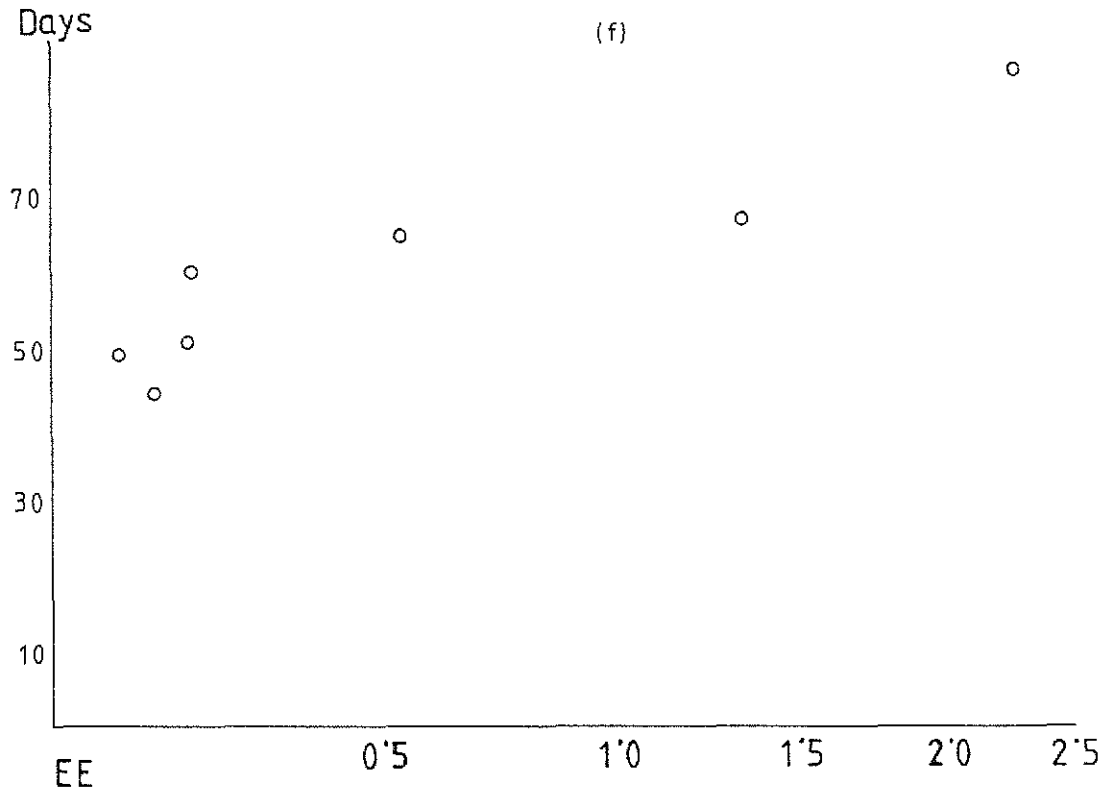

Days
(e)
70
50
30
10
EE
0·5
1·0
1·5
2·0
2·5

Fig 14f. Maximum resistance time, second instar spiderlings. Notes as for Fig 14a.


Days
(f)
70
50
30
10
EE
0'5
1'0
1'5
2'0
2'5

Concluding remarks

Theridion rufipes spiderlings take advantage of the nutritional resource of undeveloped eggs, and the benefits of this behaviour in terms of enhanced longevity and increased size (extending the potential prey spectrum) have to some extent been quantified.

Food quality and quantity were the only extrinsic variables found to markedly affect the parent female's fecundity and fertility, and even these effects were small compared to the intrinsic variations between individual females.

Egg-feeding, other than that involving trophic eggs sensu Formicidae, is in essence a harvesting phenomenon similar to cannibalising weak siblings. The mortality during the gregarious phase (after emergence from the egg sac and before dispersal) and later, resulting from starvation of weak individuals, would represent a lost resource were it not for the cannibalistic activity of the fitter spiderlings (Valerio 1977). That this behaviour does not normally operate among siblings of approximately equal vigour and fitness may relate to the potential cost of attacking such individuals compared to the benefits of success in such an encounter. West Eberhard (1975) pointed out that selection for the cannibalistic behaviour of flour beetles as described by Eickwort (1973) is more likely to operate on the mother beetle because the threshold K (cost/benefit ratio) is lower (1.0) from her

point of view than it is (2.0) from the larva's.

If parents with altruists among their brood reproduce more than parents whose brood consists entirely of selfish individuals , such altruism among brood-mates will be perpetuated despite it being detrimental to the inclusive fitness of the altruists (Alexander 1974). In the present context, a parent female may be improving her inclusive fitness by seeding her brood not with altruists but with 'food' eggs that may represent foregone reproductive units. Hence crickets (among many other animals) sacrifice some gametes or zygotes as trophic eggs to feed sibs (West and Alexander 1963). Natural selection could therefore be predicted in some circumstances to favour the polarization of broods into inviable eggs and fewer, fitter young rather than a greater number of less well adapted individuals (Valerio 1977). In this way the mean and variance of the proportion of inviable eggs, changing in response to environmental cues, in broods of spiders like I. rufipes may itself constitute an evolutionarily stable strategy. However, it would have to be demonstrated that the undeveloped eggs in such cases were truly trophic sensu strictu before such a claim could be made.

Where relatively few inviable eggs occur in a tightly-clustered brood, the allocation goes to the few individuals closest to those eggs, the result being that of a contest (by position instead of strength or wits) rather than a scramble; this may be more efficient than the dissipation of the resource through being spread

thinly among numerous individuals. Hence females who allocate yolk reserves uniformly to their eggs may be at a disadvantage.

A hypothetical example based on the present study gives an interesting outcome. Assuming 90% mortality of dispersing first instar spiderlings, a female allocating yolk evenly to a clutch of 100 eggs can expect ten progeny to set webs successfully. Consider, on the other hand, that she produces only 80 eggs of the same yolk content (and therefore with the same longevity prospects) and reduces the yolk content of the remaining 20 eggs to a level where they do not develop. From Fig 3 it seems that she will be saving at least a quarter of the volume of yolk that would otherwise have been necessary to make the 20 deficient eggs as viable as the rest. This means that she could produce five more 'normal' eggs.

She would then have 85 'standard' progeny but each would get an average of 15/85 = 0.18 egg equivalents of extra food. If these spiderlings also suffered 90% mortality on dispersal, eight or nine spiderlings would successfully set webs (compared to ten from the prefasted brood), but these would have a far longer time available to them before they must successfully catch their first prey. From Fig 14a and Fig 14b it can be estimated that 0.18 egg equivalents of extra food would double the normal starvation resistance time from about 25 to about 50 days. Prospects look better for the prefed spiderlings.

To preallocate yolk sufficient to match the longevity capability of the prefed spiderlings of the hypothetical example a female would have to increase the yolk content of each egg by 18%. Whether there are any problems or risks in producing larger-than-normal eggs is unknown, but putting 18% more yolk into the gut of an embryo may necessitate producing a slightly larger embryo. A single spiderling can be taken by definition to be 'one egg equivalent' for the purposes of this hypothetical discussion, and it can expect to resist starvation for 25 days after emergence. The provision of 0.18 further egg equivalents doubles this expectancy and it may be mechanically and/or developmentally more efficient to have this extra food available after the first molt and before emergence rather than incorporated proportionally into each egg at oviposition.

In view of the above, it is interesting that while fecundity shows no correlation with inviability or infertility, the latter have strongly skewed distributions with means of 0.110 and 0.214 and standard errors 0.009 and 0.005 respectively (Table 9). These values are at the level that would provide for an approximate doubling of the starvation resistance time of dispersing first instar spiderlings.

Table 9. Frequency distributions of INVIABILITY 1 and INFERTILITY. Corresponding mean values for the several experimental subpopulations of the study do not show marked differences.

Proportion	INVIA 1	INFERT
0.0 - 0.1	449	614
0.1 - 0.2	103	72
0.2 - 0.3	59	38
0.3 - 0.4	33	16
0.4 - 0.5	27	8
0.5 - 0.6	24	8
0.6 - 0.7	16	8
0.7 - 0.8	20	2
0.8 - 0.9	10	4
0.9 - 1.0	30	1
	771	771
Mean	0.214	0.110
Standard error	0.009	0.005
Skewness	1.765	3.362

An optimum is normally reached between producing offspring with the highest possible individual fitness and producing the largest total number of progeny at the cost of reduced inclusive fitness, and the competitive environment of immatures is a particularly important

factor in reaching this balance (Pianka 1976).

It is not known why Nephila and perhaps other spider species, whose young have been shown to be capable of feeding 12 days before they would do so naturally, do not feed on eggs (Austin and Anderson 1978). The behaviour has only to enhance the reproductive capacity of the parent female to be a potential candidate trait for selection, and it may be an efficient means of distributing resources, as discussed above.

The efficiency of concentrating reproductive resources into fewer individuals, as opposed to a scrupulously fair allocation among all the brood must, of course, be curtailed by a host of other factors that tend to push the reproductive strategy of a species towards the r end of the classic continuum; were there no check on the extent to which the sacrifice of gametes and zygotes was beneficial to the reproductive success of spiders, we would find at least some spider species that show parental care, resource concentration into relatively few young, and other typically K-selected traits (it is worth noting here that there are indeed spiders that exhibit brood care, even to the extent of regurgitation feeding, and three species of Theridion are included, T. saxatile (Norgaard 1956) and T. notatum and T. impressum (Kullman and Kloft 1969, Kullman 1969)).

Production of inviable eggs and their use by spiderlings is a topic with potential relevance to several theoretical ideas, including those mentioned above.

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APPENDICES

Appendix 1a. Sac data record sheets

Explanatory notes:

PE	= postembryos
c/l	= embryos (i.e. post-reversion, pre-eclosion), recorded under 'remarks' where appropriate
F	= fecundity
SERIES	= subfile identification codes
20*25*	= oviposition at 20° C, incubation at 25° C

Full details of feeding, vial changes, removal of egg sacs, etc. were kept in a daily 'log' for each female spider.

SERIES TR85 ♀ No. 60 Egg Sac No. 2

Feeding Status MIN Temp. 30

Ovip Date 19/3 Emer Date 29/3 Open Date 1 APR 85

Emergent Spiderlings 109 F = 116

Spiderlings in Sac - PE — Undev. Eggs - FULL —

1st 2 live stuck, 1 dead HALF 2

2nd — LT 2

Remarks

SERIES TR85 ♀No. 61 Egg Sac No. 1

Feeding Status MAX Temp. 30

Ovip Date 21/3 Emer Date 1 APR Open Date 1 APR 85

Emergent Spiderlings 48 F = 69

Spiderlings in Sac - PE — Undev. Eggs - FULL —

1st 2 dead HALF —

2nd — LT 19

Remarks

SERIES TR85 ♀No. 70 Egg Sac No. 4

Feeding Status MAX Temp. 20*

Ovip Date 10/5 Emer Date ~~NA~~ NA Open Date 23 MAY 85

Emergent Spiderlings NA F = 65

Spiderlings in Sac - PE 18 Undev. Eggs - FULL 1

1st 29 HALF 7

2nd — LT 3

Remarks *Put at 25. Opened for photography 7 c/c

Series TR85 ♀No. 79 Egg sac No. 2

Feeding Status MIN Temp. 20*

Ovip Date 15/5 Emer Date NA Open Date 31 MAY 85

Emergent Spiderlings NA F = 47

Spiderlings in Sac - PE Undev. Eggs - FULL 12

1st 1 live ok + very fat HALF 31

2nd LT 3

Remarks *25 Opened for photography

Appendix 1b. Sac data summary sheet

Explanatory notes:

Feed St.	=	feed rate
Spiders	=	emergent first instar spiderlings
C/L	=	embryos (i.e. post-reversion, pre-eclosion)
(L)	=	live
(D)	=	dead
S/M	=	stuck or malformed
Drop shock	=	rough handling, accidents
Temp. Malf.	=	temperature malfunction
Temp. Trans.	=	transfer of egg sac from 20° C to 25° C

The columns of this sample data sheet are fewer than were those on the originals (to allow for binding margins).

SAC DATA SUMMARY SHEET

SERIES

♀ No.						
Origin						
Sac No.						
Feed St.						
Temp.						
Feed-Ovip.						
Food Type						
Ovip-Ovip.						
Ovip-Emer.						
Emer-Open						
Spiders						
C/L (L)						
C/L (D)						
PE (L)						
PE (D)						
1st (L)OK						
1st (L)S/M						
1st (D)						
FULL						
HALF						
MT						
Mate F or L						
Mate-Ovip 1						
N Vial-Ovip						
Ovip-Sep.						
Drop shock						
Temp. Malf.						
Temp. Trans						
Other						

Appendix 2. Some comparable data for three other theridiid spiders. The data presented below will not be discussed in detail. Suffice to say that they lend confirmatory support to the results of the main study and suggest that similar effects may be found among many related theridiid species.

(a) Achaearanea tepidariorum

Sac sequence:

Sac No	n	Fecundity	INVIA1	INFERT
1	15	193.1	0.11	0.06
2	12	184.4	0.08	0.03
3	7	168.6	0.18	0.13
4	4	204.2	0.21	0.10
5	4	180.7	0.16	0.10

Field Seasonal:

Month	n	Fecundity	INVIA1	INFERT
Oct	3	212.3	0.08	0.08
Nov	6	181.8	0.21	0.14
Dec	4	201.0	0.05	0.02
Jan	12	194.7	0.10	0.06
Feb	3	173.7	0.24	0.07

Mean Oviposition - Emergence time in days, at 25° C:

13.71, s.e. 0.304, n = 14.

Overall mean fecundity: 187.61, s.e. 8.816, n = 45.

Overall mean INVIA1: 0.14, s.e. 0.022, n = 45.

Overall mean INFERT: 0.08, s.e. 0.013, n = 45.

(b) Acahaearanea decorata

Sac sequence:

Sac No	n	Fecundity	INVIA1	INFERT
1	11	117.1	0.24	0.18
2	10	113.1	0.23	0.11
3	6	93.0	0.43	0.12
4	4	108.0	0.31	0.20
5	2	71.5	0.32	0.26
6	1	138.0	0.17	0.17
7	2	82.0	0.23	0.18
8	1	96.0	0.10	0.03

Field Seasonal:

Month	n	Fecundity	INVIA1	INFERT
Feb	5	104.2	0.23	0.21
May	2	107.0	0.42	0.30
June	3	111.3	0.28	0.14
Oct	3	87.7	0.55	0.33
Nov	10	122.8	0.16	0.13
Dec	4	94.0	0.19	0.15

Overall mean fecundity: 105.61, s.e. 4.988, n = 39.

Overall mean INVIA1: 0.29, s.e. 0.041, n = 39.

Overall mean INFERT: 0.16, s.e. 0.022, n = 39.

(c) Latrodectus hasselti

Sac sequence:

Sac No	n	Fecundity	INVIA1	INFERT
1	38	169.1	0.30	0.20
2	30	114.0	0.31	0.21
3	20	119.0	0.28	0.21
4	16	127.1	0.32	0.22
5	10	160.1	0.26	0.13
6	9	131.0	0.31	0.18
7	5	151.8	0.28	0.24
8	5	187.8	0.26	0.18
9	4	155.7	0.21	0.14
10	2	171.0	0.14	0.11
11	2	175.5	0.41	0.35
12	2	107.5	0.67	0.57

Field seasonal:

Month	n	Fecundity	INVIA1	INFERT
Dec	7	173.6	0.33	0.24
Jan	4	138.0	0.42	0.17
Feb	6	105.2	0.41	0.33
Mar	5	153.4	0.24	0.23
Apr	2	112.0	0.34	0.32

MATEFORL

Place	n	Fecundity	INVIA1	INFERT
Field	29	137.2	0.34	0.26
Lab	7	157.7	0.22	0.19

Overall mean fecundity: 156.9, s.e. 4.9, n = 212.

Overall mean INFERT: 0.20, s.e. 0.011, n = 212.