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A description of the reproductive biology of the fishing spider *Dolomedes triton* (Walck.) (Araneae:Pisauridae) in central Alberta.

BY

Jack P. Wojcicki

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

DEPARTMENT OF ENTOMOLOGY

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled A description of the reproductive biology of the fishing spider *Dolomedes triton* (Walck.) (Araneae: Pisauridae) in central Alberta submitted by Jack P. Wojcicki in partial fulfillment of the requirements for the degree of Masters of Science.

John R Spence

John R. Spence

Bruce S. Heming

Jan O Murie

Jan O. Murie

Hugh F. Clifford

Simon D. Pollard

08/06/1992

To my father, Dr. Henry M. Wojcicki, who taught
me that learning is a never ending process,
the difference between being knowledgeable
and being able to think, the importance of compassion,
and to be proud.

ABSTRACT

Field and laboratory observations were used to study the reproductive behaviours of the fishing spider *Dolomedes triton*. Adult males emerged before their prospective mates, were attracted to freshly moulted conspecifics but did not differentiate between females in various stages of development. Males remained close to sub-adult females, but exhibited no recognizable agonism between each other during courtship or mating. Courtship involved 'tapping' and 'jerking', but not 'leg waving' or 'palpal drumming'. Males performed a ritualized 'wrapping' behaviour and 'fast-tapping'. Male courtship behaviours were most often observed in the presence of females but males also exhibited these behaviours in the absence of females and/or female borne stimuli. During copulation, males inserted a single palp, only once, using the tibial apophysis as a lever to pry open the epigynum and as a guide for the embolus. Males were capable of multiple matings, but females rarely mated more than once. Females rarely ate their mates, but after mating, became voracious feeders, attacking subsequent courting males. Female behaviour changed after mating so that courting males were perceived as food items rather than potential mates.

Field experiments show that the reproductive output of *Dolomedes triton* females is affected by both female size and food availability. Clutch size, egg sac weight and body mass increase of gravid females were limited by food availability, particularly for larger females. Ten of eleven starved females failed to produce eggs, suggesting that juveniles do not accumulate sufficient reserves for reproduction. Mean egg weight and time to develop the first egg sac were not affected by food level and showed no relationship with female size. Feeding on a male had no effect on female reproductive output so females do not derive any special nutritional benefits from cannibalism. Because smaller females were less susceptible to food limitation than were larger ones, it appears that smaller females may be at a selective advantage on ponds where food is limited, while larger females do best where food availability is high.

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TABLE OF CONTENTS

List of Tables:

List of Figures:

CHAPTER 1: GENERAL INTRODUCTION

Many recent studies of animal behaviour are descriptive and fail either to assign function to, or establish the adaptive significance of the behaviours described (e.g. Fraser 1987). In contrast, other studies of behaviour are so focused on determining function, that comprehensive behavioural descriptions are neither included nor referred to (e.g. Kessler 1971). Neither of these approaches are, in themselves, wrong, indeed both are necessary parts of the scientific process. However, a complete analysis of behaviour should include: a) detailed behavioural description b) definition of proximate function and, if possible c) establish the ultimate function or selective advantage of the behaviour. A comprehensive description of the behaviours observed is necessary to provide a background for any conclusions relating to function (e.g. Elgar 1991). Understanding the connections between observed behaviours and their functions provides significant insight into questions about ecology, evolution and physiology.

Reproduction in spiders has been studied using both functional and descriptive approaches. Both have led to a greater understanding of the evolutionary pressures which shaped the mating systems seen in this group of animals (e.g. Jackson 1980; Robinson & Robinson 1980; Killebrew & Ford 1985; Elgar & Nash 1988; Starr 1988). Though general patterns can be seen in the mating systems of spiders (see Robinson 1982), there is a great deal of variability among and even within taxa (Jackson 1980). Studies of deviation from and/or similarity to general trends in reproductive biology indicate how and which selective pressures have affected the evolution of mating systems.

The fishing spider, *Dolomedes triton* (Walck.), is common throughout North America and is the most aquatic species of the nearctic members of the genus (Carico 1973), inhabiting the shoreline of standing and flowing bodies of water (Zimmermann & Spence 1989). Though this species is conspicuous and its populations can be quite large, there has been only limited work on its biology, and no study treats its reproductive biology in a comprehensive manner. Carico (1973) provided a systematic description of this species which included some descriptions of biology. Roland & Rovner (1983) provided the first descriptions of some of the courtship behaviours of *D. triton*. They also studied vibratory and chemical communication and the relationship of these behaviours to courtship. Further study on the importance of the vibratory aspect of courtship was done by Bleckmann & Bender (1987). Bleckmann has performed several studies on the sensory ecology of *D. triton* (Bleckmann & Barth 1984; Bleckmann & Rovner 1984; Bleckmann,1985; Bleckmann 1986; Bleckmann & Lotz 1987). Ecological studies by Zimmermann & Spence focus on prey use (1989) and population structure (1992).

This study on *Dolomedes triton* was inspired by three questions. First, females of this species are entelegynes, (spiders having separate copulatory and fertilization ducts), and I ask if this morphological characteristic has shaped the evolution of communicatory behaviours and the mating system in general, as has been suggested by Austad (1984) and Jackson (1986). Second, could the extensive use, and the associated selective pressures, of an aquatic habitat be responsible for specialized reproductive behaviours of *D. triton*, and could these behaviours also affect the mating system of this spider? Finally, does the use of a habitat which is often ephemeral affect female post-mating strategies and reproductive output?

Thus, the objectives of this study were to provide a comprehensive description of the reproductive behaviours of *D. triton* and to determine their function with respect to the selective pressures of an aquatic habitat and entelegynous females.

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CHAPTER 2: THE REPRODUCTIVE BEHAVIOURS OF *DOLOMEDES TRITON*

INTRODUCTION

Mating systems in spiders include sequences of behaviours which may be quite complex. Three aspects of reproductive biology which contribute to this complexity are female genital structure and sperm use, adaptations to the habitat, and courtship and its function(s).

Sperm use in spiders is determined by female spermathecal structure. Haplogyne spiders have a common copulatory and fertilization duct while entelegynes have separate copulatory and fertilization ducts (see Foelix 1982 and Austad 1984). The differences in female spermathecal structure has been suggested as an important determinant of spider mating systems (Austad 1984; Jackson 1986; Eberhard *et al.*, MS). There is potential for more sperm competition in haplogyne spiders because sperm from several matings are mixed. In entelegyne spiders, the first sperm received by a female is usually the first to fertilize her eggs and, hence, sperm competition is much reduced. In entelegyne spiders selection is expected to favour those males that are either the first to mate with a female, can guard their mate from further copulations, or have the ability to remove sperm from previous matings. It should also favour single over multiple matings for females.

Habitat influences the evolution of mating systems because most spiders mate on some substrate, be it vegetation or webbing (see Robinson 1982). For spiders to copulate on the water surface would require several modifications to both behaviour and structure because spider courtship and copulation involves a good deal of leg and body movement on the part of one or both sexes.

Courtship in spiders is comprised of any behavioural interactions between sexually mature individuals before mating (Robinson & Robinson 1980). The basic function of courtship in spiders has yet to be determined (see Robinson 1982). Its most likely functions are to inhibit female predatory behaviour and/or to provide a basis for mate choice (Starr 1988) both of which require specialized behaviours which, through selection, add to the complexity of mating systems.

Although the fishing spider *Dolomedes triton* occurs throughout North America (see Chapter 1), the only work on its reproductive biology was done in eastern North America (Roland & Rovner 1983, Bleckmann & Bender 1987). Preliminary observations in western Canada suggested that there were differences between the mating behaviours of eastern and western populations. In addition, work by Zimmermann and Spence (1989) suggested that males of *D. triton* are subject to sexual cannibalism and this could have important, unstudied implications for the evolution of mating behaviour.

My intent in this study was to describe and analyze the reproductive behaviours of *D. triton* as observed in central Alberta, to document the frequency of sexual cannibalism, to compare observed behaviours with existing descriptions of *D. triton* behaviour, and to suggest hypotheses about the selective advantages of these behaviours. I performed field and laboratory observations to answer the following questions: 1) How do males find females? 2) What are the selective advantages of the behaviours which make up courtship? 3) How does *D. triton* copulate and what are the functions of the males' unique structural features (i.e. the tibial apophysis on the palps and the femoral spur on leg IV)? 4) Do females eat their mates?

OBSERVATIONS & EXPERIMENTS

Observations and experiments on the reproductive behaviour of *D. triton* were made in both the laboratory and the field. Although laboratory work allows greater control and detail of observation it does not always duplicate reality and, therefore, field observations were conducted as a check on generalizations drawn from laboratory observations. If observations from the laboratory differed from those from the field, then the laboratory observations were discounted. If, however, laboratory and field observations were seen to be the same then the information was pooled.

Observations in the laboratory were carried out using laboratory-reared adults during the winter months of 1988 and 1989. Spiders were housed in either circular, 4 litre tubs or in glass aquaria (approximately 25 cm^2 per spider). Clean pieces of

Styrofoam™ were used as substrates and spiders were fed sarcophagid and muscid flies and house crickets (*Gryllus* sp.).

Field observations were made from mid-May through July 1987 to 1989 at three ponds at the George Lake Field Site (114°06'W, 53°57'N) about 100 km northwest of Edmonton, Alberta, Canada. These ponds are described elsewhere; for Gate Pond see following chapter, for Experiment Pond see Spence (1986), and for Meadow Pond see Zimmermann & Spence (1992). Spiders observed on these ponds were residents and were individually marked as described by Zimmermann & Spence (1992).

The description and analysis of reproductive behaviour is presented for each of the following four phases: 1) male searching, 2) courtship, 3) copulation, and 4) cannibalism. I used names of previously described behaviours (Roland & Rovner 1983) where possible. For undescribed behaviours I assigned names based on empirical descriptions (Lehner 1979) so as not to presume function.

MALE SEARCHING BEHAVIOURS

Methods & Results

i) Field Observations

METHODS: Male searching behaviours were observed from mid-May to mid-June during the period when males were moulting to the adult stage on the ponds. Twenty-five marked males were each followed for five minutes and their behaviours were continuously recorded. Only active males, initially separated from all conspecifics by at least 0.5 m, were chosen for observations.

RESULTS: The behaviours observed are described in Table 1.1. In general, males moving across the water surface periodically skim the surface or tap on a substrate with legs I and/or I and II (the combination of these behaviours is called 'chemoexploration' by Roland & Rovner, 1983). Whether a male skims or taps is dependent on the surface he is moving over. Skimming occurs on water while tapping occurs on solid substrates. After chemoexploring, males usually perform the 'jerk' behaviour which produces a signal wave as described by Roland & Rovner (1983). This sequence of 'movement - chemoexploration - jerk' made up the searching routine of males. The searching routine was observed from one to three times for each male during the five minute observation period (1 routine = 13, 2 routines = 8, 3 routines = 4) and was seen in 93% (38/41) of the five minute observation periods. Following execution of these behaviours, males would either become quiescent for 2 to 5 seconds (75% of the observations) or continue moving (25% of the observations). Only three of the 41 observed searching routines did not follow the typical sequence of behaviours. In two cases the males were distracted by movements of gerrids near them, and once a male was frightened away by a tent caterpillar (*Malacosoma disstria*) dropping onto the water surface near it.

On several occasions I saw a number of adult males in association with penultimate stage females, but because these females move around a great deal I did not collect any data about cohabitation. At no time during these associations was inter-male aggression observed.

ii) Laboratory Experiment

METHODS: In the laboratory I performed an experiment to test the ability of male *D. triton* to differentiate between females in various stages of reproductive development. Females used were of the following stages: ante-penultimate females (N = 6), penultimate females (N = 6), virgin females (N = 6), mated females (N = 4), and females with egg sacs (N = 4). I used 50 x 25 cm aquaria with partitions secured across the centre of the aquaria, forming two 25 cm^2 sections, and with screened lids. Water level in the aquaria was maintained at ca. 12 cm. and the water was constantly aerated using an electric air pump and air stone. Four different types of partition were used to identify what cues, if any, males use to differentiate between female stages: 1) A solid, clear plastic partition (25 x 30 cm), which completely separated the two halves of the aquarium from top to bottom and side to side, was used to test the importance of sight only; 2) A partition of black screen (21 x 28 cm, mesh size ca. 0.8 mm^2) on a narrow frame of plastic (25 x 30 cm), offering poor visibility but permeable to water, was used to test for water-borne stimuli; 3) A short (3 cm above water surface), solid, clear plastic partition (25 X 15 cm) was used to test for air borne stimuli; and 4) As a control, the aquaria were not divided into halves by a partition. A circular piece floating Styrofoam™ (dia. = 6 cm) was placed in each half of the aquarium for the spiders to rest upon. Females were allowed to become resident on one side of the partition (12 to 24 hours).

Males were then introduced to the compartment opposite from a female, and I recorded what behaviours were performed, the time to the first performance of a behaviour, the sequence of the behaviours, and the orientation of the male while performing these behaviours. Pairs were observed for 15 to 30 minutes each with each partition type. A total of 5 males were tested with 26 females. As a control, males were also tested in clean aquaria with fresh water and all types of partitions but without females.

RESULTS: Males performed searching behaviours regardless of the type of partitions used. The orientation of the male when performing searching behaviours was directed towards the female in only two situations. First, when the screened partition was used and the female was resting on or near the screen the male moved toward her with greater accuracy and as he neared his behaviours became more intense. The condition of the female, however, made no apparent difference to male behaviours. Second, where no partition was used, the males frequently encountered a dragline laid down by the female and followed it. They followed in the direction of the female only 49% of the time (56/114) and their behaviours did not intensify until they came within 5 cm of the female, regardless of her condition. In all cases, including the control situation, males performed the same behaviours in the same sequence as was observed in the field. Searching males chemoexplored the water surface before performing the jerk behaviour, pause, and then continue moving.

Discussion

Searching by male *D. triton* is made up of three phases that I characterize as 'moving', 'sensory', and 'advertising' (see Figure 1.1). The function of the moving phase is to increase the encounter rate with relatively sedentary females in a discrete habitat. Because females are not found in a particular spot (e.g. web or nest), the males must find the females. Also, males do not form territories and must go to where the females are.

During the sensory phase males home in on females. This phase is intimately related to the moving phase as the two are often performed simultaneously. Males not only move about the water surface but they are able to tell when they are near a potential mate. This aspect of searching, therefore, indicates that searching by males is somewhat directed in the final stages as males do not simply bump into females.

Finally, the advertising phase may be used by males to differentiate themselves from potential prey (Bleckmann & Bender 1987) so as not to be eaten by a virgin female (see 'Cannibalism' section below). Therefore, this behaviour can be considered to function in species recognition, not for the male to recognize the female, but rather for the female to recognize the courting male. The jerk behaviour is likely to be species-specific, and when performed near other males attracted their attention. In the field, searching males were observed on several occasions to move towards other males searching on the water surface and particularly to those performing the jerk behaviour.

The laboratory experiments demonstrated that males will perform these behaviours even without a female-borne stimulus. Although discrimination among females of different stages was not observed in the laboratory, field observations suggest that the behaviour of the males becomes more intense in response to conspecifics nearing ecdysis and to freshly moulted females. This intensified searching behaviour involves more tapping, skimming and jerking bouts. Males were also observed to react intensely to the shed skins of penultimate and ante-penultimate stage females and also to the shed skin of a penultimate stage male. The stimulus for the expression of intense searching behaviours in males may be linked to the recognition of moulting conspecifics and might be as simple as a response to the odour of a moulting related chemical. Males may move about, performing general searching behaviours without any specific stimulus. When they encounter a moulting-related chemical, their search becomes more intense. The significance of these behaviours is that it allows males to find freshly-moulted, virgin females.

Though observations in the field indicated that males associate with females, it is difficult to say if this association is cohabitiation. Cohabitation as defined by Jackson (1986) requires that males remain with a penultimate stage female until she moults and matures. *D.triton* females tend to be rather active moving around the periphery of a pond until just prior to their moult to the adult stage, making observations of cohabitation rather difficult. The few observations made on cohabitation in *D. triton* (Wojcicki, unpbl.; Zimmermann, unpbl.), however, suggest that this species is much like other entelegyne spiders (Austad 1984) and shows an attraction to, and subsequent association with, females nearing ecdysis. Determination of whether or not cohabitation occurs in *D. triton* will require future data on the integrity of adult male/penultimate stage female associations over time and space.

COURTSHIP

Methods

i) Field Observations

Fifty pairs of spiders were observed performing courtship behaviours in the field between mid-May and late-June. Owing to the large populations of adult *D. triton* on the study ponds at that time, it was not difficult to find pairs (or groups) in the early stages of courtship and to record the sequence of behaviours performed.

ii) Laboratory Observations

In the laboratory, observations were made on spiders housed either in aquaria (25 x 50 cm) or in round tubs (dia. = 25 cm). Females were provided with two or three pieces of synthetic sponge as a substrate and were held in the same container a minimum of two hours before introduction of a male. Only laboratory-reared, virgin females were used, but since both laboratory-reared and field-caught males were used, their reproductive status was not always known. As with the field observations, I recorded which behaviours were performed and their order of performance. Over 150 pairs of spiders were observed.

Results

There was no apparent difference in the courtship behaviour of 'field' and 'laboratory' males so the results were pooled. However, several differences were noted from Roland & Rovner's (1983) previous description of *D. triton* courtship. Neither 'leg-waving' nor 'palpal-drumming' were observed in my study. Instead, I observed mainly 'tapping', 'jerking', 'fast-tapping' and 'wrapping' during courtship (Table 1.2). The latter two behaviours have not been previously described for this species. The 'flip' behaviour performed by males is either the very last courtship behaviour or the very first behaviour involved in copulation. I choose to describe it here.

In addition, three female behaviours were observed. 'Swatting' was observed to be a rejection behaviour exhibited towards a courting male (Table 1.2). 'Leg curl' and 'no reaction' were behaviours that at particular times (see Figure 1.2) were necessary to sustain male courtship behaviours and indicated female receptivity.

The sequence of courtship behaviours observed in *D. triton* is presented in detail in Figure 1.2. In general, as a male approaches a female the amount of tapping and jerking increases. Upon contact, both individuals may engage in short bouts of leg interplay involving any or all of the first two pairs of legs. If the female is not receptive she will swat at the male forcing him to retreat and re-approach. If the female is receptive the male begins to fast-tap on her legs and body and moves onto the female's back. The female performs the leg curl behaviour pulling her legs in towards her body. The male then orients himself so that his abdomen is positioned above the female's first two pairs of legs. Wrapping occurs in this position with the male moving his abdomen from side to side bringing his spinnerets in contact with the female's first two pairs of legs. Silk strands may or may not be attached to the female's legs. Ninety-six observations were made of the wrapping behaviour. In 46% (44/96) no silk was attached to the female's legs, in 51% (49/96) some silk was attached, and in only 3% (3/96) was enough silk attached to the female's legs that she struggled to break free. After the wrapping behaviour, the male flips the female onto her back by pulling up with his front legs on one side while pushing down on the other side of the female with the tubercle on femur IV and reaching his palpus towards her epigynum. Any movement by the female will cause the male to either stop or jump off the female and attempt to remount her.

Discussion

The courtship behaviours of male *D. triton* are very similar to their searching behaviours. These behaviours are, in fact, not discrete repertoires but rather part of a continuum of reproductive behaviours and, hence, similarities should be expected. The number of similarities of behaviours from one aspect of reproduction to another is, to a large part, determined by the function of the behaviours. It is far more economical to retain a behaviour for a different function, or to slightly alter an existing behaviour to suit a new function, than to develop a brand new behaviour. This appears to have happened twice in the reproductive behaviours of *D. triton.*

The tapping behaviour, observed during searching, gives way to fast-tapping during courtship, an example of a slight alteration of a behaviour. Fast-tapping on the female's body induces her to leg-curl and, as has been suggested for *Pisaurina mira* (Bruce & Carico 1988), puts her into a cataleptic state. *D. triton* females did indeed become very unreceptive to other stimuli, such as prodding with a probe.

The wrapping behaviour may also help place the female into catalepsy. Wrapping is not effective in restraining a female nearly twice the size of the male, and very few males laid down enough silk so that the female struggled to break free. Most males laid down only three to four strands of silk and some males only went through the motions of laying down silk. Therefore, it seems that the function of wrapping has been evolutionarily altered from one of restraint to a ritualized behaviour possibly associated with putting the female into a cataleptic state. Similar behaviours have been reported for other spiders. For example, Starr (1988) reported that males of the spider *Dictyna volucripes* moved their abdomen as they walked over females, suggesting that they may be lightly binding the female with silk. As with *D. triton*, this 'light binding' is more likely to be a ritualized courtship behaviour than protection against sexual cannibalism.

The 'jerk' behaviour is performed exactly as it was during searching, even if the male is on the female. Though the function may still be one of species recognition it may be a way in which the male demonstrates his fitness or, as it is performed between bouts of fast-tapping, it may be connected with putting the female into a cataleptic state.

Why the courtship behaviours of *D. triton* in these populations differed from previous observations is unclear. *D. triton* does not share its habitat with any other species of *Dolomedes* in central Alberta. Even where *D. triton* occurs in the same area as *D. striatus*, the micro-habitats appear to be partitioned between the species. It may be, that without another similar species, some of the behaviours necessary for species separation are not required. A detailed study of geographical variation of the reproductive behaviours in this species would help to resolve the function of different behavioural patterns used in courtship.

COPULATION

Methods

Observations of copulation in the field were made on 27 pairs of spiders found engaged in courtship. In the laboratory, copulation was observed in 128 pairs of spiders either housed in round tubs or aquaria as described above. In both the field and laboratory, the following observations were recorded: 1) use of the tibial apophysis of the males' palp and general positions of the individuals, 2) palp use (number of insertions per copulation and number of palps used per copulation), 3) length of copulation, and 4) number of copulations per individual.

Results

There were no differences observed between copulations in the field and laboratory. A total of 155 copulations were observed. The tibial apophyses of the males' palps function both as a 'crowbar' and as a guide. During copulation the males were located at a right angle to females. The palp used for copulation corresponded to the side of the female which the male was reaching over (e.g. right side - right palp). This resulted in the tibial apophysis being situated posterior to the epigynum and the medial portion of the palp being immediately above the epigynum. The palp was turned so that the tibial apophysis was brought along the female's abdomen until it contacted the epigynum. The leading edge of the apophysis was then inserted under the epigynum. Males often required a few attempts to achieve this. Once the apophysis was in position, a final turn of the palp (clockwise for the right, counter-clockwise for the left) pried open epigynum. The ventral side of the palp then pointed directly up and with the tibial apophysis in this position it acted as a guide for the hematodochae as this expanded into the female's genital tract.

Without exception, copulation involved the insertion of a single palp, only once. Males attempted to mate on the other side of the female only if he was unsuccessful at achieving a palp/epigynum link on the first side he tried. Palpal insertions were of short duration (mean = 25.5 ± 1.1s, range = 2 - 86). Though not rigourously tested, males appeared to require a refractory period of several hours before they were able to mate again. If males mated more than once in a day they generally alternated palps from one copulation to the next. A laboratory male, which mated 6 times over a nineteen day period, alternated palp usage from one side to the other only if there had been less than 24 hours between copulations. This male would not, however, mate at all until at least 6 hours after his last copulation. Males can mate several times, but the amount of sperm transferred during these latter copulations is unknown. Females were observed to mate only once with one exception. One laboratory mated female was observed to mate a second time in the field.

Discussion

Spider copulatory positions have been grouped into four basic types (see Foelix, 1982). *D. triton* employs a modified 'type 3' position for copulation. In a standard type 3 copulation, the female stands on a substrate and turns her abdomen to one side or the other while the male reaches over the corresponding side with a palp. The differences in the copulation of *D. triton* are probably adaptations for mating on the water surface. During mating on a substrate, a female can brace herself against the actions of the male, and similarly, the male uses the substrate to anchor his actions. On the water surface, however, as a male reaches under a female the female rolls on the water surface. The male's femoral tubercle and the fact that the female is in a state of catalepsy greatly facilitates rolling the female onto her dorsal surface.

The elongated male tibial apophysis may also be an adaptation for mating on the water surface. Because they are so highly aquatic, females of *D. triton* may maintain a tightly closed epigynum. For the male to insert the embolus of his palp, and to gain access to the female's genital tract, he would have to be equipped with a structure to open the epigynum. In *D. triton* this structure is the tibial apophysis but this is not its only function. Using the apophysis as a 'crowbar' results in the ventral aspect of the palp being directed away from the female. The tibial apophysis is necessary to guide the embolus between itself and the base of the cymbium of the palp into the female genital tract.

Females of most spider species mate more than once (see Robinson 1982). Wiklund and Forsberg (1985) give several reasons why single matings benefit some pierid butterflies, and similar reasoning explains why *D. triton* females generally mate only once.

Firstly, in a species where males do not contribute anything other than sperm during mating (e.g. spermatophore and/or parental care), and if one copulation is all that is required to fertilize all of a female's eggs, then females should derive no additional benefit from mating more than once. In that case, there is no selective advantage to a female devoting energy to extra matings which are of little or no benefit. Male polygyny is favoured when a male supplies no benefits to a female, and when the male's sperm supply is sufficient to fertilize several females (Thornhill and Alcock 1983). In *D. triton*, therefore, it is likely that females receive all the sperm they require for fertilization from a single copulation, and that males contribute no benefits other than sperm to the female. This explanation does not, however, consider possible effects of genetic variability on fitness which, especially in a species that does not exhibit strong mate choice, might favour polyandry.

Secondly, the reproductive success of a female is proportional to the amount of time spent on egg-laying activities. In spiders this consists of acquiring enough food to produce eggs (see Chapter 3) to construct an egg sac. *D. triton*, and pisaurids in general, also produce a nursery web which requires considerable time, energy and effort. Finally, to maximize this time, females should mate very soon after moulting to the adult stage.

CANNIBALISM

Methods & Results

i) Field & Laboratory Observations

METHODS: Pairs of spiders that were seen copulating in the field were not disturbed at termination of mating and the frequency of cannibalism was documented. Similar observations were carried out in the laboratory, although if a female chased and/or caught a male I attempted to save him. I documented the extent of 'wrapping' whenever possible to determine if the wrapping behaviour allowed males to escape more frequently.

RESULTS: Significantly more males were captured after mating in the laboratory than in field ($\chi^2 = 4.2$, $df = 1$, $p < 0.04$). In the laboratory 39 of 128 males were caught while only 3 of 27 were captured in the field.

I also observed 4 ovigerous females eating males. These observations were made after the males had already been captured and no information was available about the behaviours leading to the capture. No observations were made of freshly moulted females eating males except where copulation was involved. The behaviours of females capturing males differed between those who captured males after copulating with them and those who captured males well after mating. It appeared that females attacked prey that struggled on the water surface from a greater distance ca. 15cm, whereas males courting these mated females were allowed to approach within 5 cm before being attacked. Females often oriented towards a courting male but waited until he came near before attacking.

ii) Release Experiment

METHODS: In this experiment individual females were either put onto the pond, and allowed to acclimatize for 10 min before an individual male was released within 10 cm (50% of the trials) or, the females were released within 10 cm of males found on the pond. Female releases involved 30 virgin females, 30 mated females and 10 females with egg sacs; 25 males were released. The behaviours and interactions of both sexes were recorded. Observations lasted 15 minutes or until a copulation was observed, the female captured a male, or the individuals wandered apart.

RESULTS: There were no differences noted in the interaction based on which sex was released. Of the 30 interactions involving virgin females, 17 resulted in copulations. Among these, 3 males were captured by females after mating. Six females neither copulated nor captured the male within the 15 minute observation period and 7 females escaped and were not resighted. Of the 30 mated females released without egg sacs, 9 captured a male, 13 did not and 8 escaped. These results indicate that significantly more mated females caught males than did virgin females ($\chi^2 = 4.5$, $df = 1$, $p<0.04$). No copulations and no male captures were observed in interactions involving females carrying egg sacs.

Discussion

In the laboratory, post-copulatory cannibalism was much more frequent than in the field. This likely occurs because males in the laboratory had nowhere to run and the female had no problem sensing vibrations on the water surface produced by males at such a close distance.

The release experiment demonstrated that mated females can be important predators of males as has been suggested by Zimmermann and Spence (1989). This corresponds with data on the population dynamics of *D. triton* in central Alberta. Numbers of males in a population decrease dramatically as females reach the adult stage (Zimmermann & Spence 1992), even though males are capable of living up to eight weeks in the laboratory.

Field observations and results of the release experiment, revealed that the behaviour of females changed after mating. Bleckmann & Bender (1987) showed that females can and do differentiate between courting males and prey items. They suggested that this differentiation functions to keep males from being recognized as food items. Because mated females often oriented towards a courting male, but waited until he came near before attacking, it is likely that the females use the ability to differentiate between courting males and other prey items to gain access to males as food.

It can be argued that some males of *D. triton* experience sexual cannibalism if sexual cannibalism is defined following Buskirk *et al.* (1984) when "a female kills and feeds upon her mate during or following copulation". Males of *D. triton*, approaching a female, evidently are unable to tell if the female has mated, and they approach and court any female discovered as a potential mate. Although killing and consuming a male without copulation does not satisfy the definition of sexual cannibalism as presented by Buskirk *et al.* (1984), it is, on an intersexual level, very close to that condition because of the effort being expended by males courting mated females in an attempt to copulate with them. The function of courtship in this species, therefore, cannot function primarily to inhibit female predatory behaviours.

It seems odd that males do not discriminate between virgin and mated females, because males that could discriminate should be at a selective advantage. It is quite possible that the act of mating triggers unreceptivity in females, which is correlated with predatory behaviour towards males. Similar behaviours are seen in salticids (Jackson 1980). This unreceptivity may be induced by either a chemical transfer from male to female as in muscid flies (Murvosh *et al.* 1964) or possibly by tactile stimuli (Jackson 1980). Regardless of how or why these cannibalistic behaviours occur, mating results in a behavioural change that enables females to utilize a new food source, namely, males. Alternately, females may be reducing competition for their progeny by killing off potential mates for other females. Zimmermann and Spence (1989) observed that predation on *D. triton* females or juveniles accounted for 37% of the cannibalism by females they observed. If a mated female feeds on other females and large juveniles, likely to become females, she removes the potential progeny of these females as competitors to her own progeny.

SUMMARY

Searching for mates by males of *D. triton* involves three behavioural phases; moving, sensory and advertising. These behaviours, especially advertising, function not only for mate location but also for interspecific recognition. Males may form associations with penultimate stage females in an attempt to secure matings with females immediately upon their moult to the adult stage.

Male courtship involves tapping, fast tapping, jerking, and ritualized wrapping. Tapping and jerking are performed no differently than during searching. Fast tapping appears to be a modified version of tapping that is, along with wrapping, used exclusively during courtship. These behaviours function together to place a female into a cataleptic state which aids copulation. Female courtship behaviours consist of swatting, which indicates female non-receptivity or rejection of the male. Leg curling and no reaction indicate that the female is receptive or accepts the male.

Male structural adaptations (elongate tibial apophyses and tubercles on the femora of leg IV), coupled with the male's ability to place the female into a cataleptic state, enables copulation to occur on the water surface. Copulations are very short relative to those of other spiders, and involve single insertions of only one palp. Males may mate several times while it is rare for females to mate more than once.

Sexual cannibalism is rare. Mated females undergo a behavioural change after mating and subsequent courting males are perceived as unique food items. Males can not differentiate between mated and virgin females and, hence, are caught and eaten by mated females.

Table 1.1: Ethogram of the searching behaviours of male *Dolomedes triton*.

Behaviour	Description
1) Walk	Slow locomotion on vegetation or water surface.
2) Row	Slow to moderate locomotion across open water; the first and fourth pairs of legs are in front of, and behind the body respectively while the second and third pairs of legs provide propulsion by moving anterior to posterior when in contact with the water surface.
3) Run	Rapid locomotion across the water; all legs involved in propelling the spider forward giving it the appearance of hopping.
4) Tap	Legs 1, and sometimes 1 & 2, are lifted a short distance above the water surface and the distal elements are alternately raised and lowered (1 to 4 taps/second); the legs may be in contact with the water, some substrate, or another individual.
5) Skim	Legs 1, and sometimes 1 & 2, are moved slowly from side to side with the distal elements just barely in contact with the water surface; may occur in conjunction with rowing, walking, or while sitting motionless.
6) Jerk	Partial flexion and extension of legs 1, and sometimes 1 & 2, while in contact with the water surface resulting in a downward thrusting; this produces a noticeable single or double concentric wave moving across the water surface.

Table 1.2: Ethogram of the courtship behaviours of *Dolomedes triton*.

MALES

Behaviour	Description
1) Tap	As described in Table 1.1.
2) Fast Tap	Essentially the same as the 'Tap' behaviour, but performed very rapidly (10 to 15 taps/second) so that the distal elements of legs I and II appear to tremble.
3) Jerk	As described in Table 1.1.
4) Wrap	Male orients himself so that his posterior end is above female's anterior end, then he proceeds to move his abdomen from side to side touching the female's first two pairs of legs. During abdominal movements, male may attach strands of silk onto the female's legs from side to side.
5) Flip	When the male reaches his right palp between the female's right legs II and III, the following 'match-up' of legs is observed: male's left palp holds proximal portion of right leg II, male's left III and IV hold distal portion of female's right legs I and II, male's right legs I and II pull up on female's right legs III and IV, male's right legs III and IV push down on female's left legs I and II. In this final leg 'match-up' the femoral tubercle on the male's leg IV is hooked onto the female's leg II. The result of first pushing down by the male's right legs III and IV and the subsequent pulling up by right legs I and II, left legs III and IV and left palp causes the female to be flipped over onto her back allowing the male to reach his right palp towards the epigynum.
FEMALES	
1) Swat	A downwards flexion of a leg or legs, primarily one of the first two pairs, directed towards, and often contacting, the male.
2) Leg Curl	A slow flexion of the proximal joints of the legs bringing the distal elements of the legs closer to the body. In this position the legs are more vertical than horizontal in their attitude.

Figure 1.1: Flow chart of male searching behaviours observed in *D. triton*. (PF = penultimate female; AF = adult female)

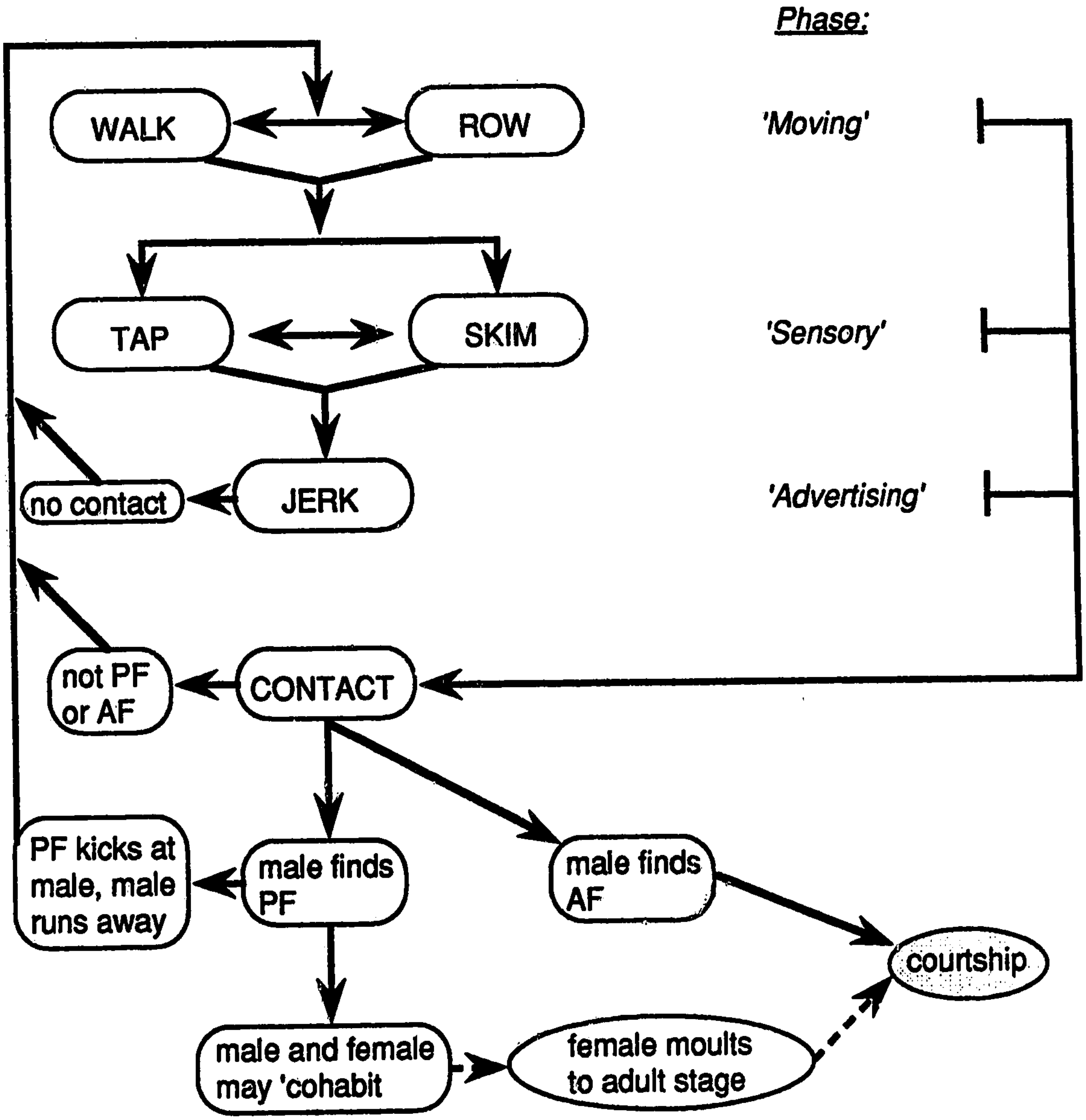
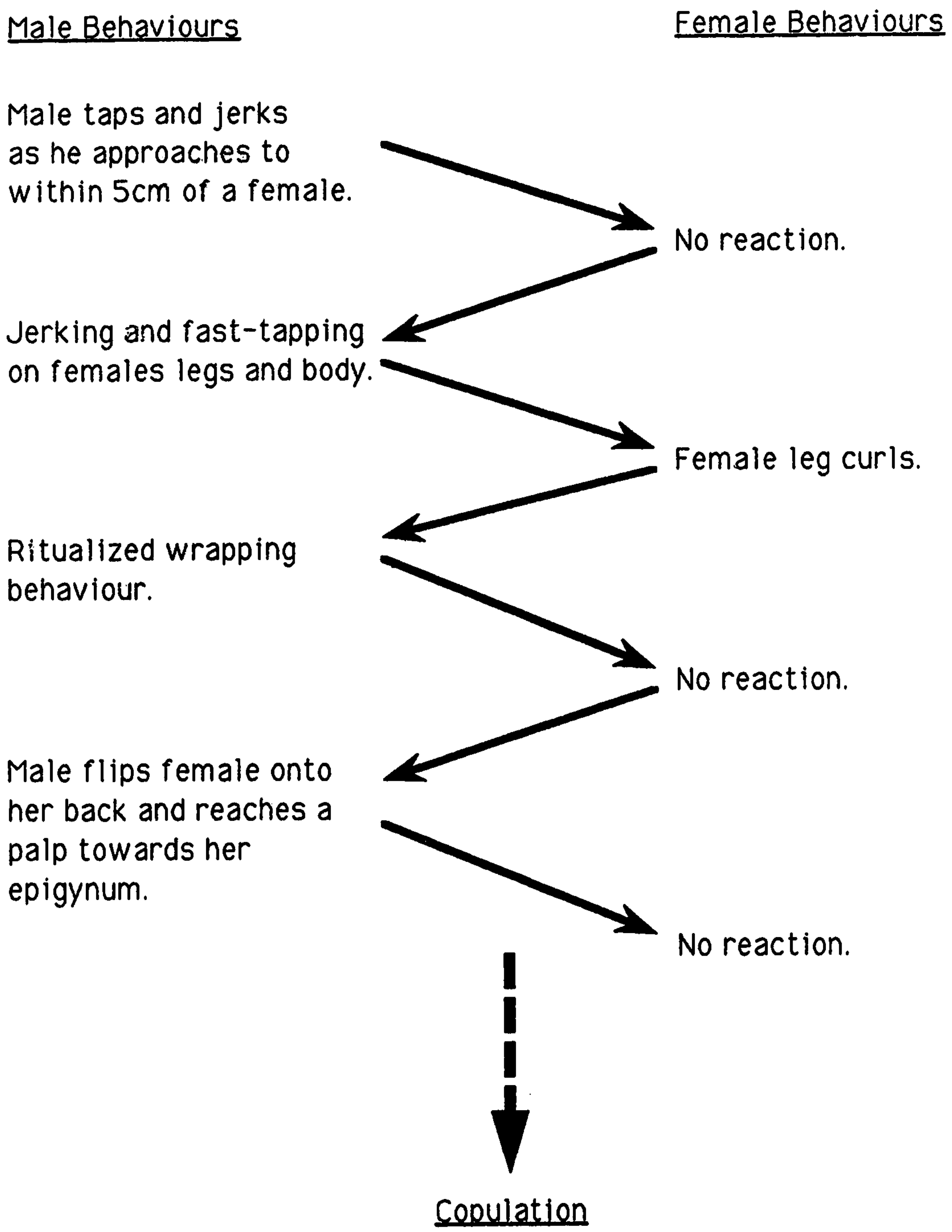


Figure 1.2: Courtship Behaviours Of *Dolomedes Triton*



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CHAPTER 3: THE EFFECTS OF FOOD LIMITATION ON REPRODUCTIVE OUTPUT IN THE FISHING SPIDER *DOLOMEDES TRITON*

INTRODUCTION

Darwin (1871) proposed that increased female size allows the production of more offspring and thus larger females should be favoured by natural selection. Many invertebrate species appear to demonstrate this relationship. In spiders, for example, strong positive relationships between female size and fecundity have been documented in *Nephila clavata* (Miyashita 1986), in araneids (Wise 79), in desids (McLay & Hayward, 1987), and in lycosids (Petersen 1950). Shine (1988) pointed out that, although greater size presents the potential for increased fecundity, larger size can only occur if energy is not limiting. Wise (1975, 1979) and Miyashita (1986) have found that fecundity in spiders is positively correlated with food availability. Therefore, the relationship between female size and fecundity should depend on food availability.

The purpose of this study was to examine relationships among food availability, body size and reproduction in a common nearctic fishing spider *Dolomedes triton* (Pisauridae). Populations of this spider include individuals that are noticeably variable in size but the implications for reproductive output are unknown. Because females of *D. triton* feed voraciously after mating (Zimmermann & Spence 1989) and increase conspicuously in mass in association with egg sac production, it seems reasonable that female reproductive output could be sensitive to food limitation.

Though intraspecific predation does occur, there is little in the arachnid literature to either support (however, see Elgar & Nash 1988 and Elgar 1991) or deny (see Buskirk *et al* 1984) the theory that the reproductive output of females is increased by feeding upon males. Although females of *D. triton* are cannibalistic (see Chapter 2 and Zimmermann & Spence 1989), it is unknown whether they derive nutritional benefit from cannibalism that is reflected in reproductive output.

I performed field experiments to answer the following questions: 1) Is the reproductive output of this spider limited by food availability? 2) Is there a relationship between female size and reproductive output? 3) Are males important food items that contribute to the reproductive output of this spider?

MATERIALS AND METHODS

Study Site

This study was done on Gate Pond, a man-made pond, at the George Lake Field Site (114°06'W, 53°57'N) about 100 km northwest of Edmonton, Alberta, Canada. The depth and area of the pond varies seasonally and annually, but the basin is *ca*. 7 m x 11 m with a maximum depth of 1 m. Cattails (*Typha latifolia*) and giant bur-reed (*Sparangium angustifolium*) grow throughout the pond and clumps of sedges (*Carex* sp) and rushes (Junaceae) surround it. The pond has harboured a large population of *Dolomedes triton* since at least 1981 (J.R. Spence pers. comm.). In 1989 the number of adults on the pond was estimated to be 200 individuals.

Methods

Experiments designed to assess the impact of food availability on female reproductive output were run from June to September in 1988 and 1989 during the period of egg sac production by *D. triton*. Spiders, provided with differing amounts of food, were held in 1 m wide x 2 m long x 1 m deep cages, each subdivided into eight-equal sized compartments (volume = 0.5 m^3 each). Each compartment was screened (mesh size = 0.8 mm^2) on the bottom and sides and had a screened lid kept in place with Velcro™. Cages were placed into the deepest part of Gate Pond and the water depth inside the cages was maintained at *ca.* 0.25 m by sliding the frame up or down on the corner posts.

Spiders were collected from various ponds in central Alberta (Table 2.1) as juveniles, reared to the adult stage and mated in the laboratory. Mated females were individually marked with Silka™ fabric paint applied on the carapace as a series of dots (Zimmermann & Spence 1992) and then divided into groups based on carapace width (group mean ± 0.16 mm). At least one female from each group was randomly assigned to each of the following experimental treatments: field control (ambient food level) (FC), male fed (MF), high food supplement (HF), low food supplement (LF), and food deprivation (FD) (Table 2.1).

Each female in the HF, LF, and FD treatments was placed into a separate compartment and held until death or termination of the experiment. Females subjected to the HF treatment were provided with three adult damselflies (Lestidae or Coenagrionidae), four adult or late instar gerrids (*Gerris* spp.), and six adult flies (Sarcophagidae or Muscidae) per sampling period (i.e. once every three days). Females in the LF treatment were fed one damselfly, one gerrid, and 2 adult flies per sampling period. These food items were chosen because they are major components in the diet of *D. triton* (Zimmermann & Spence 1989). Partially eaten or dead food items were replaced every sampling period. Spiders subjected to food deprivation (FD) did not receive any food except for the few small aquatic inverterates that managed to get into their compartments.

Females in both the MF and FC treatments were marked and released onto the pond to forage on whatever was available. However, the MF females were allowed to feed on one conspecific male after they had mated. The MF treatment was run only in 1988. An equivalent number of resident adult females were removed from the pond so that competition for food between experimental and resident spiders would not be increased.

Every three days all of the spiders from the cages, and any spiders from the FC and MF treatments that could be found, were caught, narcotized with CO_2, weighed on a Mettler™ 450 pan balance and then returned to either their compartment or to the pond. Each day between sampling dates, 6 - 18 man/hours were spent searching for missing FC and MF females and any that were caught were also weighed before being returned to the pond. These data were used to estimate increases in female body mass. When an egg sac was first discovered it was taken from a female, weighed and frozen for subsequent analysis. All females were returned to the pond on the day of capture. The experiment continued until all of the captive and free-ranging spiders had died.

The egg sacs were subsequently opened in the laboratory and the eggs counted. The silk sacs were moistened with water, compressed into small balls, wrapped with aluminum foil to minimize static charges, dried and then weighed on a Cahn™ electrobalance. The following variables were measured or calculated for each female and egg sac: carapace width, egg sac mass, mass of egg sac silk, clutch size, mean mass per egg, days from mating to production of first egg sac, and rate of female body mass increase. The mean mass per egg was calculated as '(egg sac mass - mass of egg sac silk)/clutch size', and female body mass increase was taken as '(female mass at last sighting prior to egg sac production - female mass after mating)/days from mating to production of first egg sac'. The eggs were also checked for parasites, and when possible scored for fertility. An egg was judged to be fertile if either an embryo or a germ band was visible.

Descriptive statistics, regressions, and correlations were calculated on an Apple Macintosh™ computer using the Statview 512+ package (BrainPower Inc.). Analyses of variance, using female size as a covariate, and range tests, when applicable, were done using SPSSX (SPSS Inc. 1983), and analyses of covariance for comparison of regression lines were run on the MIDAS statistical package (Statistical Research Laboratory, University of Michigan, 1976).

RESULTS

A) Number & Seasonal Variation in Egg Sacs

The analyses presented here use pooled data from 1988 and 1989 because no significant differences were found between years for any variable. Initially 83 spiders were included in this experiment. However, some of the FC and MF spiders (5/36, and 1/9 respectively) were not recaptured, and some of the caged spiders died before termination of the experiment (HF 3/19, LF 1/10, FD 10/11), thus bringing the number of spiders available for most analyses of reproductive output to 65.

Females of *D triton* produced up to three egg sacs during the experiments. Production of egg sacs was unaffected by female size or by feeding treatment except in the FD treatment where significantly fewer females produced egg sacs ($\chi^2=28.9$, $df=3$, $p<0.001$).

There were few differences between first and second egg sacs. FC females had significantly more eggs in their first egg sac (mean = 252 ± 16.1) than in their second (mean = 183 ± 17.0; *F*=6.69, *df*=1, *p*=0.013), and HF females took longer to produce their second egg sac (mean days = 17.3 ± 1.25) than to produce their first egg sac (mean days = 12.9 ± 1.24; *F*=4.86, *df*=1, *p*=0.04). Analysis of the effects of food limitation was limited to data from the first egg sacs because later in the season females were subjected to different environmental and possibly physiological factors that were not measured but could have affected egg sac production, even though such effects were significant only for the FC treatment.

B) Feeding Treatments & Size Effects

Reproductive output was affected by amount of food available but effects depended on female size. Larger females from the FC and HF treatments produced significantly more eggs and heavier egg sacs than did smaller females (Figures 2.1a-b). Body mass increase, though not statistically significant, followed a similar trend (Figure 2.1c). Although none of the regressions for the LF treatment were statistically significant their slopes were all negative (Figure 2.1), suggesting that under food limitation, the measures of reproductive output for larger females were equal to or less than those of smaller females in that treatment. In fact, two of the largest females in the LF treatment (CW = 5.6 mm and 6.1 mm) did not produce egg sacs and one large female (CW = 5.8 mm) died prior to egg sac production. Number of days to egg sac production was unaffected by food availability, female size, or by any relationship between food and size.

Feeding on a male had no positive effect on any measure of reproductive output. In fact, MF females took significantly longer to produce egg sacs (F=14.65, df=1, p=0.002) and showed smaller body mass increases (F=28.01, df=1, p=0.013) than did FC females (Figures 2.2 and 2.3) although no biological explanation is offered for these effects. No other variables were affected by female size or by feeding on a male.

Mean egg mass was unaffected by treatment, size of female, or any relationship between treatment and size. There was also no correlation between mean egg mass and clutch size indicating that larger clutches are not made up of smaller eggs. Therefore, it seems that females of *D. triton* produce eggs of relatively consistent size (0.78 ±0.03 mg) and adjust reproductive output only through changes in clutch size.

C) Food Limitation in the Field

Data from this experiment can also be used to determine if spiders on Gate Pond were food limited. Females in the HF treatment were clearly fed to satiation because live food was found in their enclosures at the end of virtually all sampling periods. During these same periods females in the LF treatment, with the exception of some smaller individuals, consistently ate all of the food items provided to them. Analysis of covariance revealed no differences between the FC and HF treatments, in either slope or Yintercept, for clutch size, egg sac mass or, body mass increase. Thus, reproductive output of the free-ranging females on Gate Pond was apparently not food limited.

D) Parasitism & Fertility

Little success was achieved in attempting to score eggs for fertility. Germ bands do not form within the eggs until about one week after oviposition based on observations of egg sacs of known age from FC females. Most egg sacs were taken away from the females after 3 to 6 days. Of those egg sacs that could be scored, fertility rates appeared to be quite high (>80%).

No evidence of parasitism was observed in any of the egg sacs examined in the course of this study (N=217).

DISCUSSION

Fecundity, Body Size & Food Availability

Food availability has clear effects on growth, reproductive output, and population density in several spider species (e.g. Turnbull, 1962; Wise, 1975 & 1979; Miyashita, 1986; McLay & Hayward, 1987). Generally speaking, when prey levels are high, rates of growth and reproduction increase, and consequently, population levels also rise. *Dolomedes triton* is widespread and common throughout its range (Carico 1973). On some ponds and lakes in central Alberta the species is extremely abundant while on others it is conspicuously rare or absent. Especially on ponds without fish as potential predators, variation in abundance may be related to availability of food. Thus, on ponds where food is not abundant, reproductive output will be low and, hence, population size will depend on rates of colonization from other, better habitats.

The present study indicates that reproductive output of *D. triton* females varies with female size but is also influenced by food availability. Thus, it appears that reproductive output is influenced both by conditions experienced over the 2-year juvenile period, and by female feeding subsequent to mating. When food was not limiting (HF) and under ambient field conditions (FC), the reproductive output of larger females was higher than that of smaller females (Figure 2.1). When food availability was low (LF) most of the large females showed low reproductive output or reproductive failure. The largest female that produced eggs in the LF treatment had a carapace width of 5.3 mm while much larger females in the other treatments produced eggs (see Figure 2.1). Thus, under conditions of food limitation, smaller females may experience equivalent or greater reproductive success than do large females because smaller females do not require as much energy to be reproductively successful. Indeed, extreme food limitation (FD) resulted in reproductive failure of all but one of the experimental females (Table 2.2). Adult feeding is, therefore, required for production of at least one egg sac. Body size, which is related to the food available to juvenile stages (Turnbull 1962; Wise 1975), apparently 'sets' the range of possible reproductive success.

Prey abundance is, therefore, a limiting factor for *D. triton*, but more so for larger females than for smaller ones. Larger females are at a selective advantage when food availability is high because they are capable of producing more offspring. When food is scarce, small females are favoured because they are capable of being reproductively successful when the abundance of prey is low. Thus, selection for increasing female size is countered by selection for the ability to use limited resources in a variable environment.

When food was not limiting, larger females produced larger clutches, heavier egg sacs and had a greater mass increase per day than did small females. There was no difference, however, in the number of days to produce an egg sac or in the mean mass per egg regardless of food availability or female size. This latter point suggests that the egg mass of *D. triton* eggs is constant and that smaller females or those that are food limited produce fewer rather than smaller eggs. This relationship between female size and 'optimal' egg mass has been described for other spider species (e.g. Petersen 1950 for a lycosid; Killebrew & Ford 1985 for an oxyopid). Although the eggs of *D. triton* are roughly the same mass, it is possible there are differences in the 'quality' of eggs, caused by the different feeding regimes.

Habitat Quality

Another factor that promotes the presence of small females in the population stems from the relationship between food availability, female size and life history. It has been shown in other studies (e.g. Turnbull 1962; Wise 1975), that the growth of juvenile stages is affected by food availability. When juvenile *D. triton* develop on ponds where there is an abundant food supply, they should become large adults. If the abundance of prey on such a pond decreased, the reproductive output of large females will fall. In the FC treatment all females, both large and small, produced eggs. Although prey abundance is high on this pond, small females persist even though they are not as fecund as larger females. Females that remain small, either through developmentally flexible responses to food level, or because of genetic differences, and that are capable of at least producing some offspring, would maintain the *D. triton* population on a pond after prey abundance falls.

Spiders that develop on ponds with low prey abundance have two options if they are to reproduce successfully: 1) become small adults, or 2) move to another pond with more food. Adults very rarely emigrate. Of over 600 adult spiders marked on three ponds, over three years, for this and other studies, only one adult female was resighted on a second pond (in this instance, ca. 40 m away). Therefore, one would expect the evolution of developmental plasticity, with respect to body size, and perhaps the ability for habitat assessment in dispersing spiderlings.

Cannibalism

It has been reported (Elgar & Nash 1988; Elgar 1991) that females of some spiders receive a significant benefit from sexual cannibalism. However, females of *D. triton* rarely eat their own mates (see Chapter 2), a condition necessary for this form of parental investment to be selectively advantageous. Males are most often consumed by females that have already mated so cannibalized males would obtain no 'parental investment' through their sacrifice. In my experiments, females did not receive any benefit, in terms of increased reproductive output, from cannibalism of males. However, because the emergence of males and females is staggered, it is possible that cannibalistic females may remove competitors, both for themselves in the short term and for their young in the long term, by assuring that late emerging females are not fertilized. Earlier emerging females may eat enough males so that later emerging females have difficulty finding a mate and subsequently do not reproduce.

SUMMARY

This study indicates that the reproductive output of *Dolomedes triton* females is affected by food availability but only in conjunction with female size. When food is abundant, larger females are at a selective advantage. In times of low food availability large females do not achieve their full reproductive output, whereas smaller females are relatively unaffected. In *D. triton* females, therefore, smaller size allows for successful reproduction at lower food levels. While this is not in agreement with Darwin's female size/fecundity model, it does demonstrate the influences of energy limitations on this relationship

Females of *D. triton* in central Alberta are not food limited because large females are reproductively successful. Female size is influenced by the food available to the juvenile stages and, ultimately, affects reproductive output. The persistence of small females within populations may be because of the ephemeral nature of the habitat of *D. triton*.

Feeding upon a single male did not affect female reproductive output in any positive way. Females, therefore, do not receive any special nutrient supplements from the male.

Table 2.1: The number and source of spiders used in the food limitation experiments, and the years in which particular treatments were run.

Date	Total # of spiders used	Treatments run	# of spiders per treatment	Spider source*
June 22, - Aug. 29, 1988	42	Field Control	15	1,2,3,5
		High Supplement	8	1,2,3,5
		Low Supplement	10	1,2,3,5
		Male Fed	9	1,2,3,5
July 19 - Sep. 8, 1989	43	Field Control	21	1,2,4,5
		High Supplement	11	2,4,5
		Food Deprivation	11	2,4,5

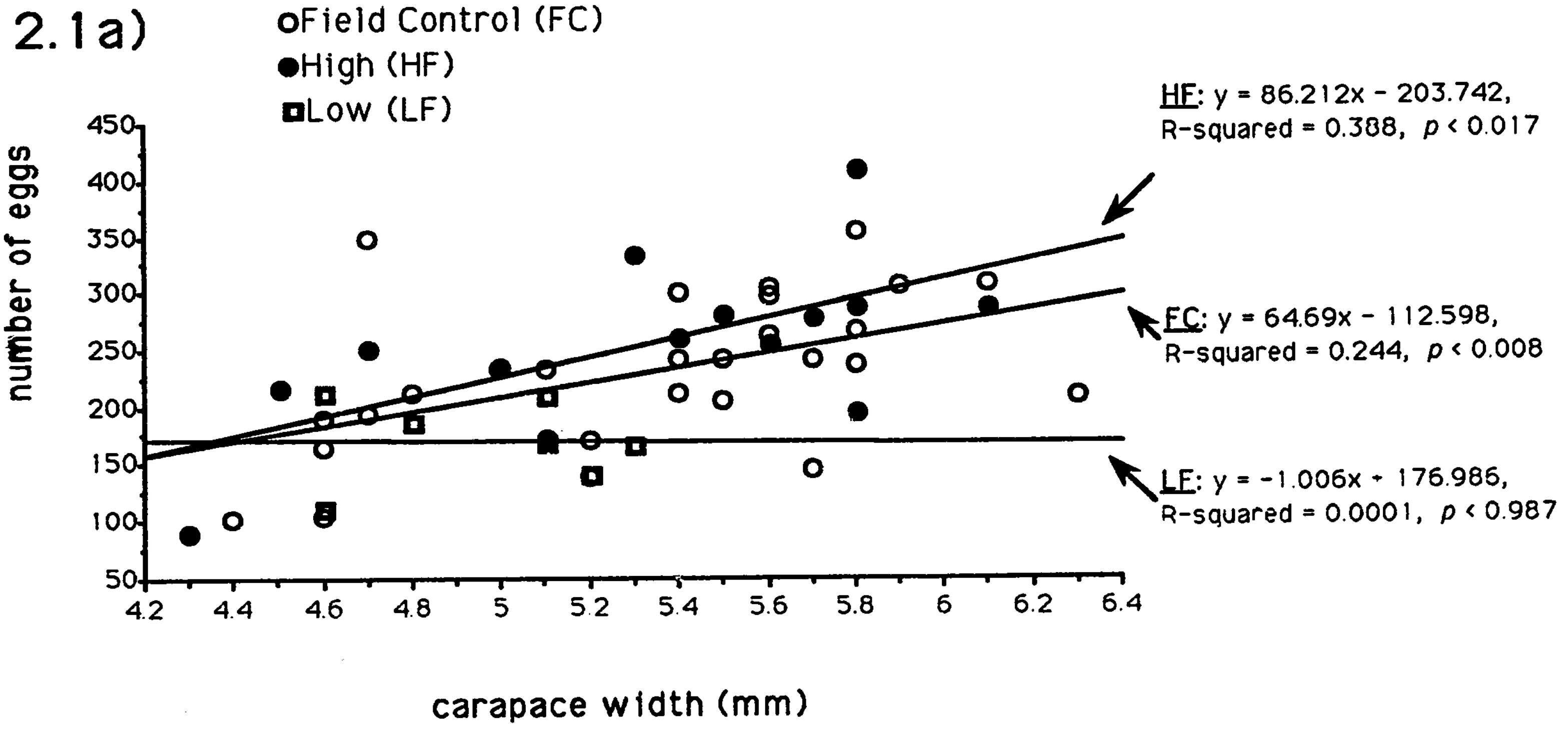
* 1=Edmonton area, 2=George Lake area, 3=Rocky Mountain House, Alberta 4=Tomahawk, Alberta, 5=Laboratory reared.

Table 2.2: Percentage of females producing first egg sacs in each experimental treatment.

	Treatment			
	FC	HF	LF	FD
%	86	84	70	9
N	31/36	16/19	7/10	1/11

Figure 2.1: Regression lines for each treatment demonstrating the relationship between female size and; a) clutch size, b) egg sac mass, and c) female body mass increase.

2.1a)

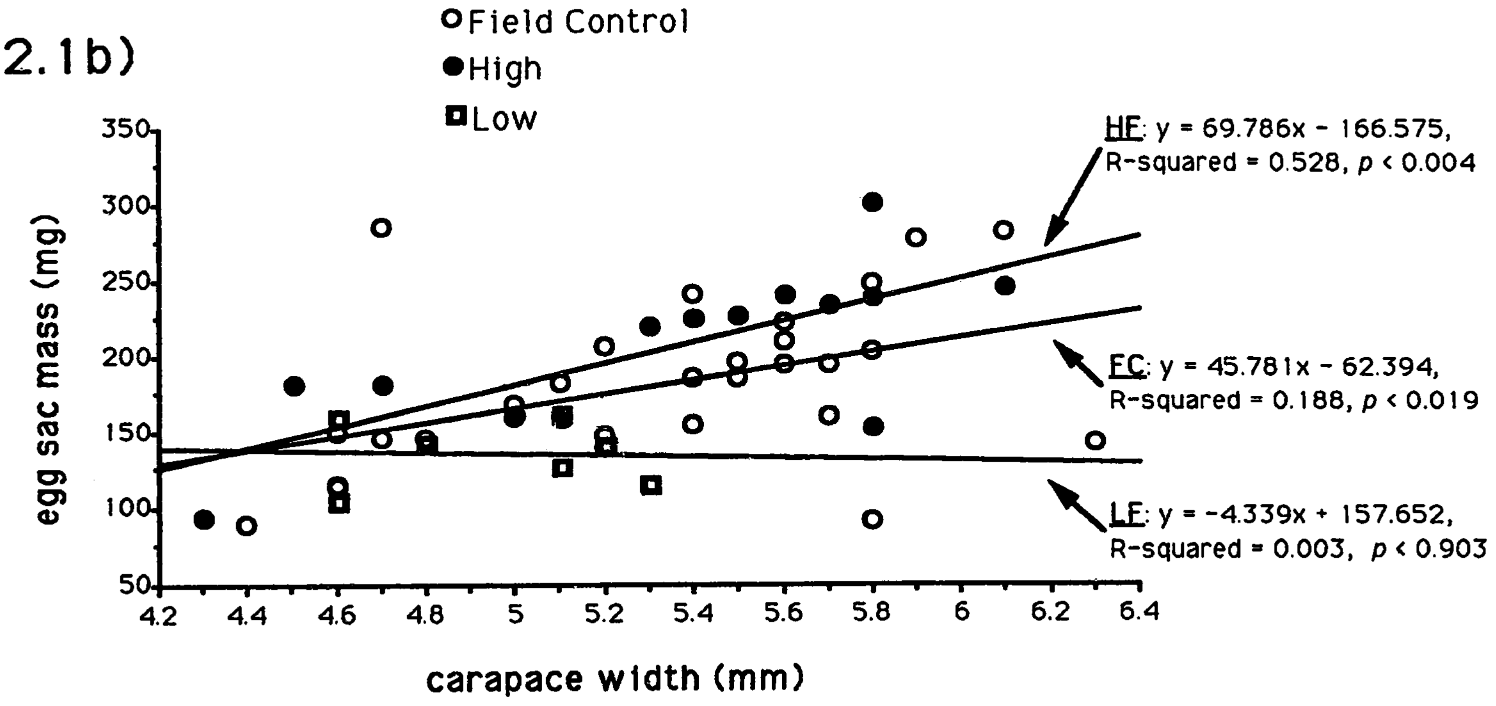


HF: $y = 86.212x - 203.742$, R-squared = 0.388, $p < 0.017$

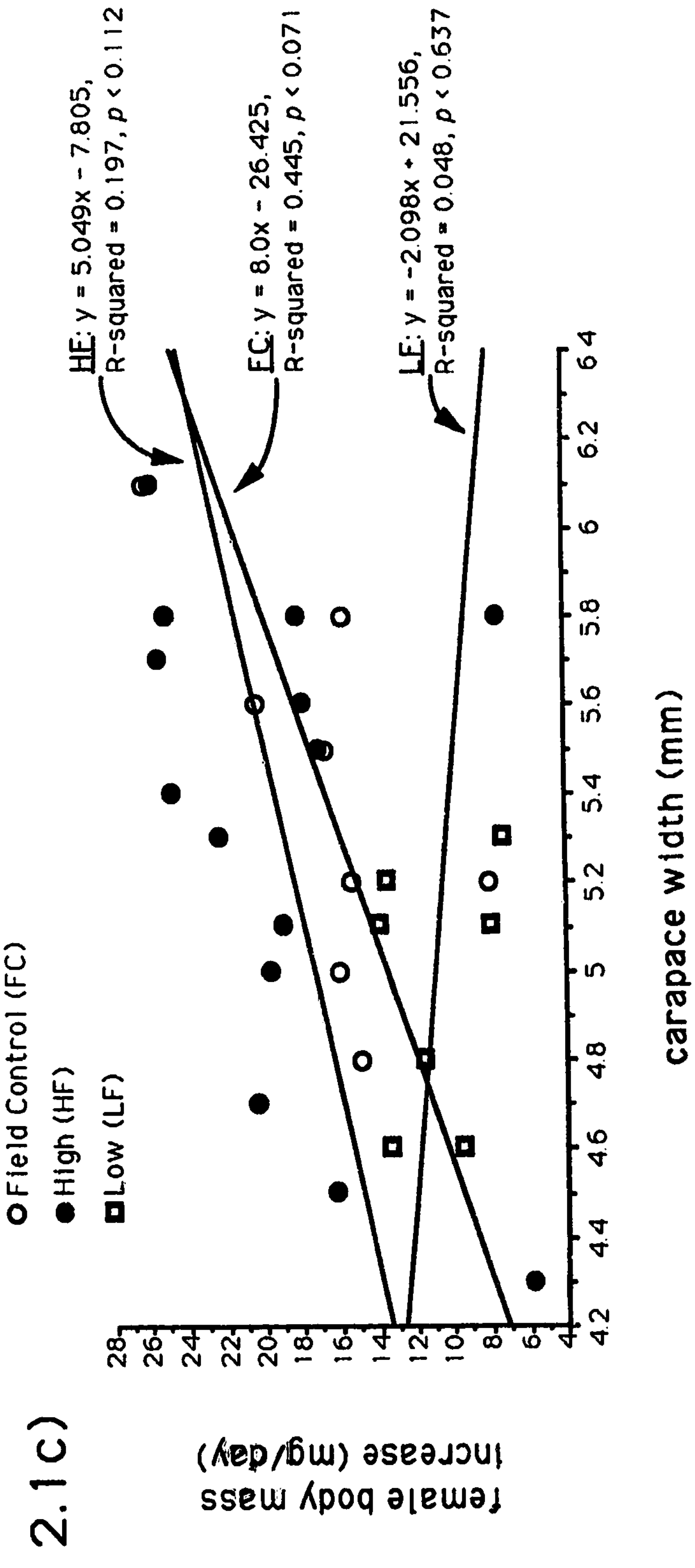
FC: $y = 64.69x - 112.598$, R-squared = 0.244, $p < 0.008$

LF: $y = -1.006x + 176.986$, R-squared = 0.0001, $p < 0.987$

2.1b)


○Field Control
●High
▣Low
egg sac mass (mg)
350
300
250
200
150
100
50
4.2
4.4
4.6
4.8
5
5.2
5.4
5.6
5.8
6
6.2
6.4
carapace width (mm)
HE: y = 69.786x - 166.575,
R-squared = 0.528, p < 0.004
EC: y = 45.781x - 62.394,
R-squared = 0.188, p < 0.019
LE: y = -4.339x + 157.652,
R-squared = 0.003, p < 0.903

2.1c)


○ Field Control (FC)
● High (HF)
▣ Low (LF)
HF: y = 5.049x - 7.805, R-squared = 0.197, p < 0.112
FC: y = 8.0x - 26.425, R-squared = 0.445, p < 0.071
LF: y = -2.098x + 21.556, R-squared = 0.048, p < 0.637
female body mass increase (mg/day)
28
26
24
22
20
18
16
14
12
10
8
6
4
4.2
4.4
4.6
4.8
5
5.2
5.4
5.6
5.8
6
6.2
6.4
carapace width (mm)

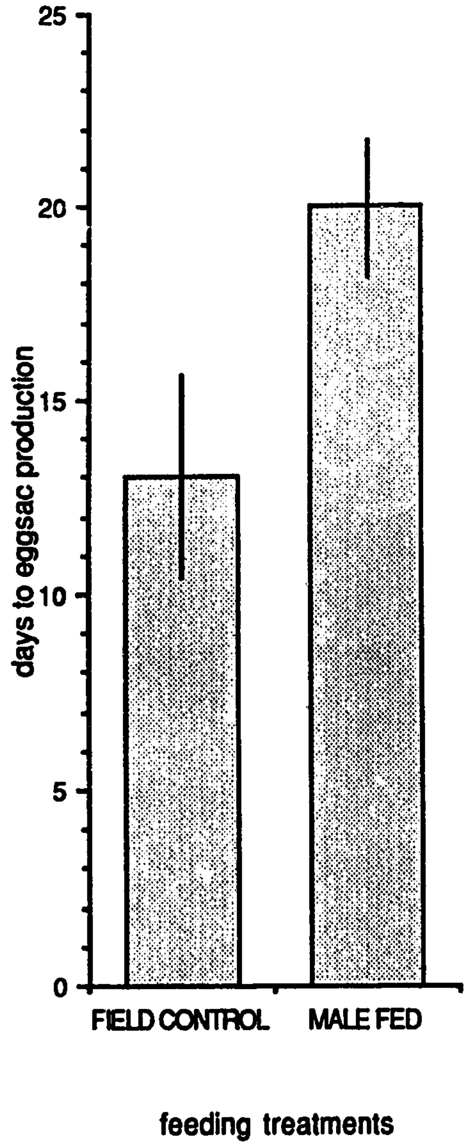


Figure 2.2: Mean number of days (±SE) from mating to eggsac production for field control and male fed females.

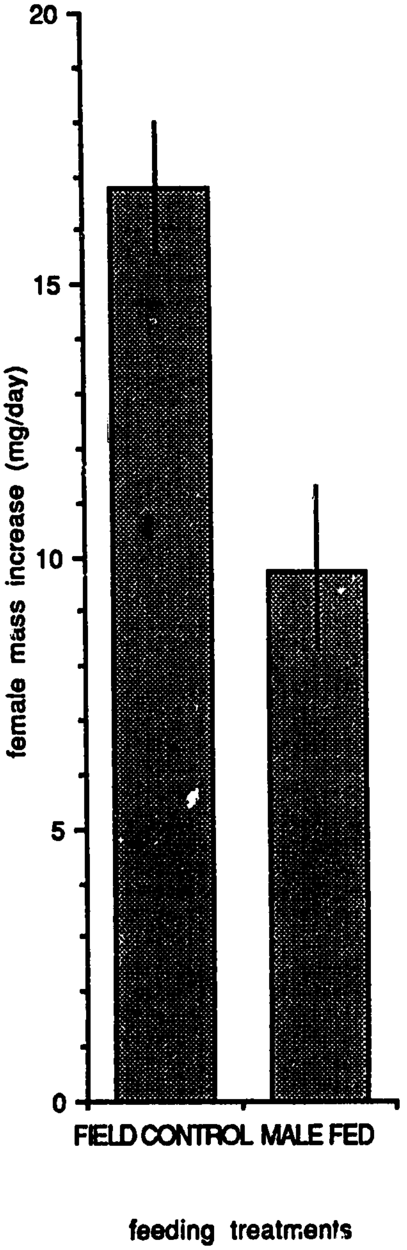


Figure 2.3: Mean female body mass increase (±SE) from mating to production of the first egg sac.

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CHAPTER 4: GENERAL DISCUSSION

The strategies underlying the reproductive biology of *Dolomedes triton* are based on maximizing the speed of reproduction for both sexes, and ensuring reproductive success in an ephemeral habitat, in the case of females. Whether these strategies are unique to the populations observed is unknown. However, the selective advantages of both of these strategies should be the same for any population of this species.

D. triton is protandrous, sensu Thornhill & Alcock (1983), (Zimmermann & Spence 1992), suggesting that males can gain access to more females by emerging earlier (Thornhill & Alcock 1983). Male reproductive behaviours have, therefore, adapted in response to the pressures of gaining the quickest access to a limited resource that diminishes over time (i.e. virgin females). This mating system most closely resembles the 'scramble competition polygyny' described by Thornhill and Alcock (1983). In this type of mating system protandry does not necessarily lead to aggressive competition between males for potential mates but, as observed for *D. triton*, may simply be a race between competitors to be the first to reach a mate.

The significance of protandry, male associations with penultimate stage females, and the ability to copulate quickly is twofold. First, the more rapidly males can copulate, the sooner they can begin searching for another female to mate with. As entelegyne spiders, the first sperm a female receives is the first used to fertilize her eggs. Therefore, a male must be the first to mate with a female, but need only mate once to stand a good chance that his genes are carried on in the next generation. If a male achieves more than one mating, more offspring will carry his genetic complement and he is, therefore, at a greater selective advantage. Females also benefit from quick copulations. Because they derive all the sperm necessary to fertilize their eggs from one mating, as would be expected in a species whose females only mate once (Wiklund & Forsberg 1985), it is more efficient, with respect to time and energy, to spend further effort on egg production rather than on further courtship and copulation.

Second, mating with freshly moulted, virgin females is important because males cannot differentiate between virgin and mated females. For an early emerging male, the best way to ensure that a female is virgin, is to remain with a penultimate stage female until she moults to the adult stage. Functionally, this behaviour very closely resembles cohabitation (Jackson 1986), which allows males to gain access to virgin females in species whose females are unlikely to re-mate. Jackson has attempted to ascribe certain characteristics, such as nest building, to those species of spiders observed to cohabit. He does caution, however, that patterns of sperm use are very important in determining which spiders should be expected to exhibit cohabitation. Observations from this study suggest that *D. triton* is much like other entelegyne spiders which show an attraction to and/or a subsequent association with females nearing ecdysis (Austad 1984).

The lack of differentiation between virgin and mated females by males has further consequences. As the females mate, males encounter an increasing number of mated females. These mated females, having undergone a behavioural change which causes them to recognize courting males as prey items, attempt to eat the males. This female predation on males is the most likely cause for the crash in the male population observed by Zimmermann & Spence (1992). Because mated females are eating courting males, it does not appear that courtship functions to inhibit female predatory behaviours. It can be argued, however, that though the mating system of *D. triton* originally is of the scramble competition type, the very act of mating constitutes an indirect monopolization of virgin females by early emerging males. The mating system then becomes more a 'resource defense polygyny' (Emlen & Oring, 1977) whereby the early emerging males are restricting access to virgin females. This is especially important because the mated females will eat late emerging males.

Once females have mated, they have all the sperm they need to fertilize their eggs. The female strategy shifts from mating to acquiring food for egg production. Females of *D. triton* are capable hunters (see Bleckmann & Lotz, 1987; Zimmermann & Spence, 1989) but, as for any predator, the best prey is the one that requires the least energy to capture. Males will approach and court a mated female as if she were a virgin. Mated females alter their normal prey catching behaviour so that males are allowed to come closer than a regular prey item before being captured, thereby reducing the amount of energy required for prey capture. Parental investment by males is discounted for the following reasons. Firstly, females are not feeding on their mates so the males are not contributing any benefit to their progeny. Secondly, female reproductive output is not benefitted by feeding upon a male.

Female reproductive output is affected by a relationship between female size and food availability. Large females require the most food but can also produce the most eggs when food is abundant. Smaller females do not produce as many eggs but do not require as much food. Persistence of small females within a population results from the ephemeral nature of the habitat. Should a pond or lake for some reason (e.g. drought, temperature, vegetation changes, *etc.*) become not productive enough to support large females, the smaller females will succeed reproductively. It may be that large females only succeed reproductively during times of plenty, and that small female always succeed, except in the harshest of conditions. Caution must be taken not to regard this as a 'group selection' theory. Females are not being small for the good of the population, rather, they are small because the amount of food they had access to as juveniles was less than that for large females. I suggest that smaller females are not being eliminated from populations because they can at times, due to the unstable nature of the habitat, achieve greater reproductive success than large females.

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APPENDIX

An overview for busy scientists and regular people.

The whole damn thing has to do with scramble competition. Males run around looking for jail-bait females to hang around with and ultimately for fresh females, possibly using a moulting related substance as a stimulus, but who knows! They might shack up for a while before they tie the nuptial knot but that's what is expected of good entelegynes these days.

The function of courtship behaviours and of fancy male bits is to speed up everything, up to and including copulation, and to be able to do it on the water surface to boot. Males have got to be quick because they can't tell a virgin from a mated female; the quicker they get done with a copulation, the sooner they can move on to another and that's the name of the game isn't it? As all the virgins get mated all the males encounter are mated females who've lost that loving feeling. The females eat the males and that's pretty much it for the males for another year.

In the meantime, females only need to mate once and then it's on to the egg making business. They've got all the sperm they need, they just need food for egg making energy. The easiest way to get a quick meal is to let it come to you, and the males so graciously do just that. They practically throw themselves into a strange females fangs. It would be so touching if the males were the examples of perfect altruism ... but that's crap. They're just food with nothing special about them, other than they're easy to catch. That's what all the food limitation stuff was about! Females that eat males don't cash in by having more eggs. It's the big females that make the most eggs but they need the most food. Little females don't make as many eggs but don't need as much food either. So if the pond goes crappers and there ain't but a little food, the little females will do just fine and there will be *Dolomedes triton* babies for another arachnologist to look at.