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# Effects of satiation and food deprivation on feeding behaviour in the pholcid spider, *Pholcus phalangioides*

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## Summary

*Pholcus phalangioides* (Fuesslin) (Araneae, Pholcidae) spins a three-dimensional tangled web. It attacks its prey by wrapping, only feeding once the prey is immobilised. The effects of satiation and food deprivation on the feeding behaviour was investigated using *Drosophila melanogaster* as prey. The feeding sequence was described using five variables. Feeding time decreased as the number of flies presented increased, but in deprivation experiments feeding time increased with time since last meal. Four other variables, response time, wrapping time, number of bites and number of escapes did not vary with degree of satiation or with time since last meal.

## Introduction

Much work has been done describing the sequence of behaviour associated with feeding in spiders. The araneids (orb-weavers) have been a particularly well studied group (reviewed in Riechert & Łuczak, 1982). Jackson & Brassington (1987) give a detailed description of the elements of the behaviour involved in prey capture in the pholcid *Pholcus phalangioides* (Fuesslin). Field experiments suggest that food is limited in natural spider populations (reviewed by Wise, 1993) and this is reflected by observed associations between spider density and prey density (e.g. Turnbull, 1964; Riechert & Tracy, 1975; Gillespie, 1981; Vollrath, 1992). However, little work has been documented on the effects of food deprivation on behaviour. Hunger in invertebrates can be defined as the weight of food necessary to return the animal to a condition of complete satiation (Holling, 1966).

*P. phalangioides* is a cosmopolitan spider occurring in and around human habitation. It builds a non-cribellate, non-sticky, three-dimensional web. It is readily distinguished by its extremely long legs and unusual defensive behaviour known as "whirling", in which it rapidly gyrates its body while keeping its long legs on the silk (Murphy, 1914; Bristowe, 1958). Little is known of the natural predators of *P. phalangioides,* though it is known to fall prey to some other spider species (Jackson, 1990). It is polyphagous, eating airborne and flightless insects and numerous species of spider, particularly those found foraging in autumn (Jackson, 1990).

Several aspects of the feeding behaviour of *P. phalangioides* were investigated in this study. First, the sequence of behaviour associated with feeding was described. This information was then used to design experiments to assess whether any part of the feeding sequence varies with the level of satiation or with the length of time since the last feed.

## Material and methods

A sample of 30 specimens of *P. phalangioides* were collected from inside buildings in the Aberystwyth area (Grid ref. SN 5881). Each spider was housed in a separate, plastic 1 l carton, with a clear window at the front. Each cage was labelled with a number, and each spider was identified by this label throughout the experimental period. Ventilation holes were added and single holes of about 5 mm diameter cut out through which food could be added. These could be closed with a flap between feeding events. Water was provided by leaving a water-soaked piece of blotting paper on the floor of the cage every 3–4 days.

The laboratory was illuminated by four overhead fluorescent strip lights, set to a 12L:12D photoperiod. In addition there was ambient glow from an incubator (100w bulb) in constant operation. The temperature and humidity were recorded throughout the experimental period. The mean ambient laboratory temperature was 20.5°C, with a range from 17–24°C. The mean ambient humidity was 39.4%, with a range of 29–44%.

### *Preliminary trials*

Preliminary trials provided information on the ethology of the feeding process and formed the basis of the sequence of prey capture outlined in Fig. 1. Spiders were set up three weeks before experiments to give them time to settle, construct a web and to familiarise them with the proposed prey (*Drosophila melanogaster*). The probability of attack may increase with familiarity with a specific prey type (Turnbull, 1964; Hardman & Turnbull, 1974). In addition, the spiders had to become accustomed to frequent handling. Initially any handling of the cages invoked the whirling response, but after some 2–3 weeks of handling, this response was greatly reduced. Four preliminary trials were carried out:

(1) Time to hit web. Flies were introduced singly to cages with webs present but with the spiders removed. The time taken for the flies to make contact with the webs was observed.

(2) A nominal feeding regime was established, with each spider fed a single fly every 3–4 days, and the sequence of feeding behaviour observed. This sequence was subsequently broken down into its constituent variables so that it could be evaluated quantitatively.

(3) A continuous feeding regime was established, each spider being fed a single fly immediately after discarding its previous meal.

(4) Multiple feeding. Here 5 flies were added to the web consecutively, so that as one fly was wrapped another was added. This was an extension of (3) so that the main experiments could be planned with known satiation levels.

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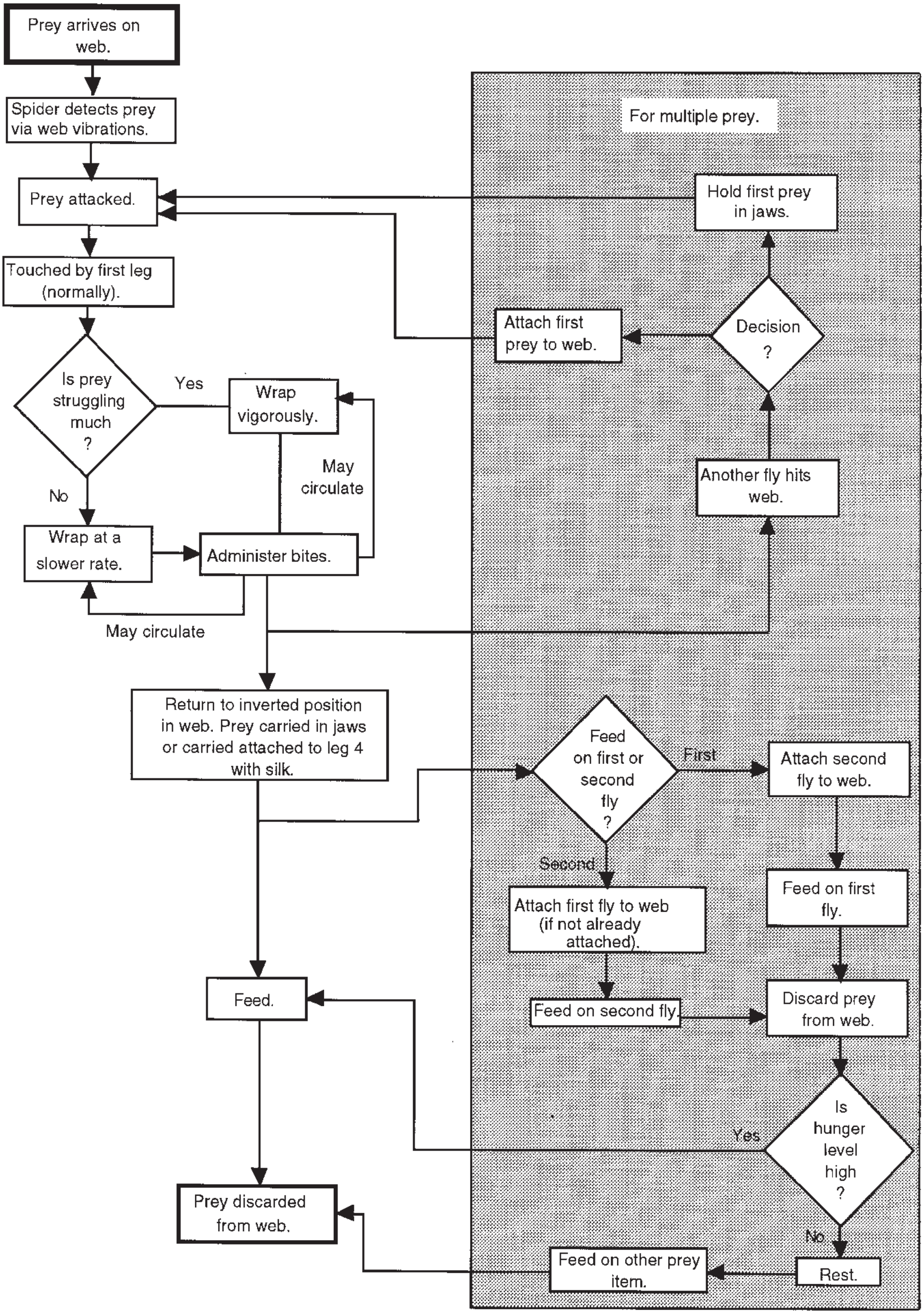

Fig. 1: Behavioural sequence during prey capture and feeding for *P. phalangioides*. Data based on 106 observations over a 9-week period. Rectangular boxes indicate events or actions, diamonds indicate decisions.

### *Effect of satiation*

A randomly selected group of 10 spiders were fed single flies continuously until the spider would capture and eat no more, up to a maximum of six flies; this was planned from the continuous and multiple feeding regimes in (3) and (4) above.

### *Effect of deprivation*

Six randomised groups of spiders ($n=5$) were established 1 week after the satiation experiment described above. Spiders were fed 5 flies initially — the "primary feed" (5 flies being the maximum number of prey taken in a day, during both continuous and multiple feeding trials). Then spiders in each of the groups were fed a single fly at a predetermined time after the primary feed — the "test feed". Some of the spiders did not catch and eat all five flies so it was assumed that spiders were satiated from a zero reference time. Test feeds, of a single fly, were carried out 18, 24, 30, 72, 96, 192 h after initiation of the primary feed and are collectively defined as the presentation sequence. The experiment was then repeated with complete re-randomising of the 6 groups 1 week later, giving trial 1 and trial 2 respectively.

### *Sequence of feeding behaviour*

The sequence of behaviour accompanying feeding was described by five components: Response time, Wrapping time, Number of bites, Feeding time, and Number of escapes from the web. The response time was defined as the time between the fly hitting the web to when the spider first started to wrap it with silk. The wrapping time was defined as the time between the initiation of wrapping to the bite that terminated wrapping. Wrapping time is closely related to the third variable, number of bites administered. These were often administered following wrapping, but were frequently interspersed with wrapping. The feeding time was defined as the time between the administration of the final bite and the time when the prey was discarded from the web. The number of escapes included vigorously struggling flies that managed to free themselves before the spider responded or reached them, and flies that were dislodged by the reactive movement of the spider.

The data were analysed by a two-factor ANOVA with period of deprivation and trials as the two factors. Correlation analysis was applied where appropriate.

## Results

*Sequence of prey capture and feeding:* The behavioural sequence of prey capture is summarised in the flow diagram (Fig. 1). Throwing silk is the primary predatory tactic of *P. phalangioides* (Jackson & Brassington, 1987), so the spider is able to attack further prey items whilst holding prey in its chelicerae.

*Continuous feeding — effect of satiation:* There was a significant negative correlation between feeding time and the presentation sequence ($r=-0.95$; $df=5$; $p<0.01$) (Fig. 2). Thus the time spent feeding decreased as the number of flies presented increased. The number of escapes was significant ($p<0.05$) but showed no significant correlation with presentation sequence and was not readily interpretable as a pattern. No other variable in the sequence showed any significant effect with presentation sequence; their means are recorded in Table 1.

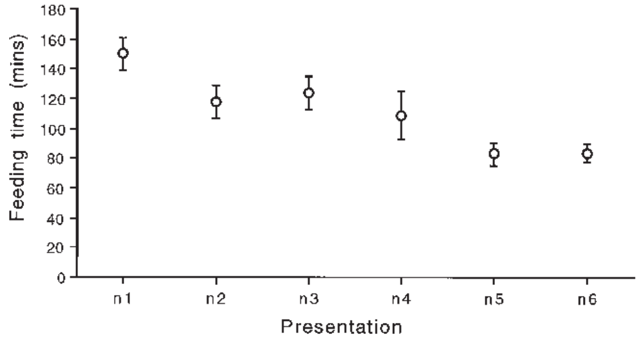

Fig. 2: Relationship between feeding time and presentation sequence in *P. phalangioides*. Feeding time was inversely related to the number of flies encountered. Means are shown with standard errors ($r=-0.948$; $df=5$; $p<0.01$).

*Effect of deprivation:* The period of deprivation had a significant effect on feeding time ($F_{5,36}=8.087$; $p<0.01$). The trial × deprivation period interaction was marginally significant ($F_{5,36}=2.778$; $p<0.05$). In both trials, feeding time increased with period of deprivation, but the pattern of increase differed in the two trials (Fig. 3). There was no significant effect of deprivation time on the four other variables analysed; their means are recorded in Table 1.

## Discussion

The sequence of behaviour outlined in the flow diagram (Fig. 1) is consistent with the detailed, descriptive, behavioural observations of Jackson & Brassington (1987). The strategy of wrapping the prey as the primary mode of attack means that the spider does not risk losing already captured prey during a subsequent attack. Members of other spider families such as araneids initially subdue their prey with a bite and then secure it to the web (Foelix, 1982). The spider's body is less vulnerable to damage from the prey, as the prey

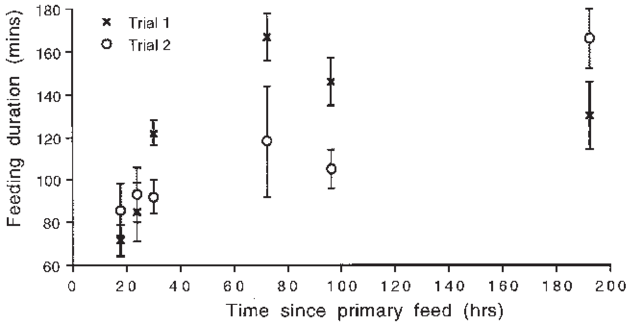

Fig. 3: Effect of length of food deprivation on feeding duration of *P. phalangioides* fed a single *Drosophila* prey. Means with standard errors. Trial 1 and Trial 2 used the same animals re-randomised with a 1-week interval between.

| Component of feeding behaviour | Continuous feeding trials | Deprivation trials Trial 1 | Trial 2 |
|---|---|---|---|
| **Response time (mins)** | 7.23 ± 2.70 | 6.88 ± 3.78 | 5.75 ± 6.65 |
| **Wrapping time (mins)** | 1.71 ± 0.28 | 2.49 ± 0.64 | 1.95 ± 0.35 |
| **Number of bites** | 3.06 ± 0.91 | 3.42 ± 1.17 | 2.36 ± 0.64 |
| **Number of escapes** | 2.80 ± 0.86 | 2.13 ± 0.87 | 2.46 ± 1.02 |

Table 1: Means of behavioural variables with standard errors.

is wrapped at a long distance from the body. Many araneids will attack large or vigorously struggling prey by wrapping (or cut them loose, if they are large or dangerous) (Foelix, 1982), presumably minimising risk of danger to the body.

The increase in feeding time with length of food deprivation in both trials (Fig. 3) was consistent with the continuous feeding trials, in which feeding time decreased with consecutive presentations of prey. This suggests that as the feeding time reaches its asymptotic value, the spider may be maximising its food returns. Givens (1978) has argued that soft body parts are more easily digested from the larger parts of the prey body, but hard parts and appendages would be more difficult to consume. Further, Haynes & Sisojevic (1966) found that only spiders starved for long periods pierced the appendages of prey. The time and energy spent extracting food are a cost that must be balanced by the benefit gained from the food. Past feeding history may influence this trade-off. The longer the period of deprivation the more likely the spider is to maximise its food intake from the next prey capture. The results from trial 1 resembled a rectangular hyperbola, but in trial 2 there was a more linear increase in feeding time with time since last meal (Fig. 3). The previous feeding history of the spiders may have caused this difference.

The first three behavioural variables in the feeding sequence (response time, wrapping time and number of bites), did not vary significantly in their respective duration and frequency with time since last meal. Many spiders have a fixed investment in the web structure before they gain any benefits in the form of prey. This investment is in the form of time and the metabolic cost of silk production (Hagstrum, 1971). Web building is largely under genetic control (Foelix, 1982), and this may well be the case with the wrapping response, as it is performed even by the younger spiders.

The number of bites and the wrapping time, although they did not vary in this study, are believed to be correlated with the size and degree of struggling of the prey (Riechert & Łuczak, 1982). Different types of prey are wrapped at different rates and for different durations (Riechert & Łuczak, 1982). Harwood (1974), Peters (1931) and Robinson (1969) (cited in Riechert & Łuczak, 1982) have shown that behavioural stimuli from the prey have a deterministic effect on predator behaviour patterns and the variability in the duration, frequency and amplitude of such patterns. Prey size is likely to affect the strength, duration, amplitude and frequency of the behaviour of prey with a consequent effect on the behaviour of the predator. In addition the variation in prey size will affect the feeding time, as larger prey would be expected to be fed on for longer. A study of the combined effects of prey size and period of deprivation would provide further information on the variability of feeding behaviour in spiders.

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