

## Temperature affects both web spider response time and prey escape speed

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### Summary

The escape time of *Drosophila melanogaster* caught in webs of the orb-weaver *Araneus diadematus* was studied in the laboratory at three different temperatures (14, 21 and 27°C). The results showed that the escape time was significantly faster at higher temperatures. Reaction time and orientation time of the spiders were slower at the lower temperatures, leading to a significantly slower overall capture speed at 14°C compared with the higher temperatures. However, the combined temperature effects on the behaviour of the prey and the predator were not additive; correlating capture and escape time gave a theoretical capture success of around 70% at 14°C and 21°C, whereas it was only around 60% at 27°C. We hypothesise that the lower capture success at 27°C is because flying insects are already warmed up but the spider, immobile at the centre of the web, has a relatively lower body temperature.

### Introduction

The evolution of silk and its use in webs and snares has proved extremely successful for spiders. Of the more than 30,000 currently recognised spider species, around 50% are sit-and-wait predators that construct silk traps of some type (Foelix, 1996). Among the web-building spiders, the cribellate orb weavers are considered to build the most efficient traps (Rypstra, 1982) as the features of their orbs have evolved to optimise prey capture (Krink & Vollrath, 2000; ap Rhisiart & Vollrath, 1994; Eberhard, 1986; Rypstra, 1982). However, there is considerable variation in web geometry between individuals as well as between subsequent webs made by the same individual (Sherman, 1994; Witt & Reed, 1965). The geometry of the orb web is influenced by a variety of factors, including the spider's age and size (Heiling & Herberstein, 1999; Risch, 1977; Christiansen *et al.*, 1962; Mayer, 1953), its nutritional state (Herberstein *et al.*, 1998; Vollrath & Samu, 1997; Sherman, 1994), recent prey experiences (Venner *et al.*, 2000; Schneider & Vollrath, 1998; Sandoval, 1994), risk of predation (Li & Lee, 2004), shape of the building site (Krink & Vollrath, 2000) and last but not least, climatic factors (Vollrath *et al.*, 1997). This variation in web design has led to the recognition that the web is more than a standardised sieve-trap. Clearly, web and spider are an integrated system where the orb web performs a range of functions in spider protection and prey capture by effectively extending the spider's body (Vollrath, 2000).

It can be deduced from the geometry of the web that the prey's escape time and the spider's capture time have

played a major role in the evolution of the orb web. The majority of vertical or near-vertical orb webs are asymmetrical, with the lower part being larger than the upper part (Heiling & Herberstein, 1999; ap Rhisiart & Vollrath, 1994; Vollrath & Mohren, 1985). A likely explanation for this is that the spider, owing to gravity, can move faster downwards than upwards (ap Rhisiart & Vollrath, 1994). The likelihood of the spider reaching its prey before it escapes is, therefore, greater in the lower part of the web, making it profitable to invest most time and energy in this part. However, the ability of the web to retain prey is strongly dependent on prey type. Considerable variation in escape time can be found for various naturally occurring prey species, with body weight and wing size being as important determinants as high levels of activity (Nentwig, 1982).

Prey-capture success does not depend only on the retention ability of the web, but also on the prey-catching behaviour of the spider. Since spiders are poikilothermic animals, their attack behaviour can be assumed to be as temperature-dependent as is the escape behaviour of the prey insect. Indeed, the results of modelling indicate that ambient temperature is considerably more important than prey density for energy gain in the desert funnel-web spider *Agelenopsis aperta* (Gertsch) (Reichert & Tracy, 1975). Another indication of the importance of temperature for prey capture comes from the orb-weaver *Micrathena gracilis* (Walckenaer), which orientates its web so as to achieve an optimal body-temperature (Biere & Uetz, 1981). Ambient temperature during web-construction is also known to affect the web geometry, both in the field (Sherman, 1994) and in the laboratory (Vollrath *et al.*, 1997).

Predatory behaviour in the orb-weavers follows a highly stereotyped sequence (Reichert & Łuczak, 1982), although there is considerable inter-individual variation between spiders (Weissmann & Vollrath, 1999; ap Rhisiart & Vollrath, 1994; Klärner & Barth, 1982). Some of this is related to experience (Turnbull, 1960), and some to the size and potential danger of the prey (Klärner & Barth, 1982; Robinson *et al.*, 1969). Here we hypothesise that some of the measured variability in prey-capture success may also depend on relative differences in the body temperatures of the "lurking" spider (relatively inert and thus cold) on the one hand and the flying prey (highly active before and even after impact and thus warm) on the other. We used wild-type *Drosophila melanogaster* fruit-flies as prey to investigate various components of the prey-capture sequence of the cross spider, *Araneus diadematus* Clerck, at three different temperatures. For each temperature the total capture time was coupled with the escape time of *D. melanogaster* from empty webs, in order to determine whether the spider's predatory success varied with temperature.

### Material and methods

#### *Experimental design: fly escape time*

Orb webs were obtained from juvenile *Araneus diadematus* (weight  $\approx$  35 mg) kept in 30 × 30 × 5 cm frames

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under standard laboratory conditions ( $24 \pm 2^\circ\text{C}$ ,  $45 \pm 5\%$  RH and 16:8 L:D). After removal of the spider the intact web was placed in front of an opening cut in a cardboard box. Wild type *Drosophila melanogaster* were released into the box and allowed to fly around freely. Some of the flies passed through the opening of the box and became entangled in the web. The escape attempts made by these intercepted flies were recorded using a surveillance camera connected to an Hi8 Sony video recorder allowing frame-by-frame playback. The wild-type flies were taken from a laboratory colony maintained at room temperature (around  $20\text{--}22^\circ\text{C}$ ) and reared on Carolina Biological *Drosophila* medium.

Upon contact with the web the flies wriggled vigorously. This activity sometimes caused the thread to break, often resulting in the fly falling down to hit the thread below and so on, causing a slow downward movement of the fly. In these cases the escape time was recorded as the time interval between first and last contact with the web. In a few cases the fly escaped from the web, but then later (within a few seconds) became entangled at a new spot in the web. Here the two capture events were treated as independent, but only the initial entanglement period was used.

Flies were recorded as caught in the web, if they were in contact with the web for more than three consecutive frames (120 ms). A total of 20 webs, with 4–9 (mean 6.2) flies recorded per web, were used at each experimental temperature. Temperatures used were 14, 21 and  $27^\circ\text{C}$ . The flies had been acclimatised to the given temperature for at least 24 h before the onset of recording and all webs used had been built within a 24-h time period before the experiment.

#### Experimental design: capture speed

Juvenile *Araneus diadematus* (weight  $\approx 35$  mg) were collected in the wild during the summer and stored in a refrigerator at a temperature of around  $10^\circ\text{C}$  until used in the experiment. Every third week the spiders were taken out of the fridge, watered and hand-fed 4–6 live fruitflies. Before the start of the experiment the spiders were removed from the fridge and put in  $30 \times 30 \times 5$  cm plastic frames separated by thin vaseline-smear plastic sheets. The frames were stacked like books on a bookshelf under our standard laboratory conditions ( $24 \pm 2^\circ\text{C}$ ,  $45 \pm 5\%$  RH, 16:8 L:D). All spiders were fed one fruit fly in their web daily during one week of acclimatisation before the experiments. The webs were then sprayed with water and cut along the edges using a hot wire, leaving the wetted web silk in the frame for the spider to re-ingest. On experimental days, webs built in the laboratory during the preceding night were transferred with the spiders in the hub to the experimental climate room in the morning. Here they were allowed at least one hour of acclimatisation before the onset of the experiment. These webs were also then placed in front of a black and white surveillance camera connected to an Hi8 Sony video recorder allowing frame-by-frame playback. *Drosophila* from the same stock as in the previous experiment were used as prey. The flies had been accli-

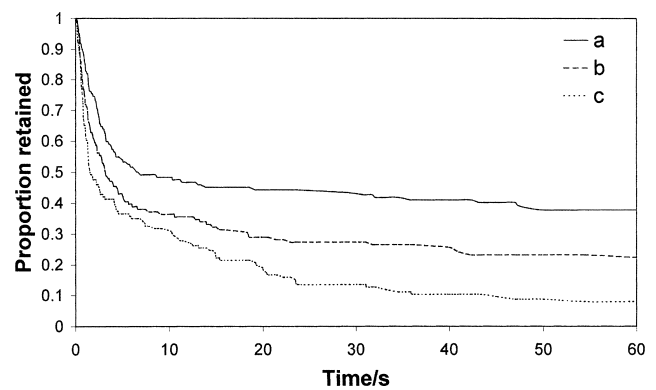


Fig. 1: The proportion of intercepted flies retained in the web (without resident spider) as a function of time. Each curve represents a different temperature: a= $14^\circ\text{C}$ , b= $21^\circ\text{C}$ , c= $27^\circ\text{C}$ .

matized to the climate room for at least 24 h before being used in experiments. One fruit fly was flicked into the lower quadrant of each web. Soft forceps were used to place the fly into the web in order to ensure it was alive and wriggling when hitting the web. Each trial was repeated at 3 different temperatures, 14, 21 and  $27^\circ\text{C}$ , with the same group of spiders (21 spiders recorded at each temperature). Three to four days elapsed between each trial, during which time the spiders were returned to the standard laboratory conditions and treated in the same way as during the acclimatisation period.

#### Data analysis

For the experiment on fly escape time, each fly was recorded for at least 60 s after being caught by the web. If the fly had not escaped during this time, the data were not used. These kind of data are equivalent to censored data obtained from survival studies. For this experiment, the non-parametric log-rank-test for comparing two or more samples was applied to compare differences in escape time at the different temperatures (Pyke & Thompson, 1986).

Four sets of data were obtained from the recordings of predatory behaviour: (1) *distance* from the spider to the prey was measured on the monitor using a ruler; (2) *reaction time*, i.e. the time elapsed between the prey hitting the web until the spider reacts and starts to turn towards it; (3) *orientation time*, i.e. the time elapsed between when the spider turned towards the prey until it left the hub; (4) *capture time*, i.e. the time elapsed between the spider leaving the hub until it touched the prey with the chelicerae. Capture speed was calculated by assuming a linear relationship between capture time and distance. In a few cases, the spider either showed no sign of having detected the fly or it oriented towards it but did not move to catch it. In some cases the spider would catch the prey after several minutes, but in other cases the prey was still untouched in the web when recording was terminated. From such observations, a cut-off point for reaction of 10 s was chosen. Thus, if the spider's turning or reaction time was longer than 10 s, the recording was excluded from the analysis. In order to approach normality and acquire equal variances all

time data were transformed using the Box-Cox power-transformation. Capture speed was transformed using the natural logarithm. Transformed data were analysed using a multivariate analysis of variances (MANOVA) for repeated measures. The Pillai-Bartlett trace criterion was used, because of its robustness to violation of assumption (Keselman, 1998). Correlations with distance were investigated using the Pearson's correlation coefficient. All statistical tests were performed using the software JMP 3.2.2 (Macintosh version, SAS Institute Inc., 1997) with the significance level set at  $\alpha=0.05$ .

## Results

### Fly escape time

Out of the 36 spiders used for the prey escape experiment, 30 built webs consistently enough to contribute one or more webs. Eight spiders contributed webs at all three temperatures.

Each fly caught in the web resulted in a minor disruption of the web geometry at the spot where it was caught. It might, therefore, be expected that, as more flies hit the web, it would be progressively easier for them to escape. However, no such trend was found for at least the first 6 flies (flies 7–9 excluded owing to few data) caught in each web (14°C: log-rank  $\chi^2=1.67$ ,  $df=5$ ,  $p=0.89$ ; 21°C: log-rank  $\chi^2=2.13$ ,  $df=5$ ,  $p=0.83$ ; 27°C: log-rank  $\chi^2=2.78$ ,  $df=5$ ,  $p=0.73$ ).

There was a difference in the shape of the prey-retention curves, with the slowest rate of escape from the web occurring at the lowest temperature and progressively higher escape rates at increasing temperatures (Fig. 1). A statistical analysis revealed that there was a significant difference between the shape of the curves (log-rank  $\chi^2=30.17$ ,  $df=2$ ,  $p<0.0001$ ), indicating that it took significantly longer for the flies to free themselves from the web at lower temperatures than at higher temperatures.

### Capture speed

In the experiment with predatory behaviour, the initial distance between the spider and the fruit fly was predicted to be constant. However, although care was taken when tossing flies at the webs, exact placement was not possible. This, together with differences in web-size, resulted in variable distances from spider to prey for each sample. The mean distance ( $\pm$ SD) at 14°C was  $62 \pm 18$  mm, at 21°C it was  $65 \pm 16$  mm and at 27°C it was  $54 \pm 14$  mm. There was no correlation between distance and reaction time for any of the three temperatures (T=14°C,  $R^2=0.29$ ,  $p=0.20$ ; T=21°C,  $R^2=0.12$ ,  $p=0.61$ ; T=27°C,  $R^2=-0.01$ ,  $p=0.95$ ) nor between distance and orientation time (T=14°C,  $R^2=0.16$ ,  $p=0.49$ ; T=21°C,  $R^2=0.10$ ,  $p=0.67$ ; T=27°C,  $R^2=0.15$ ,  $p=0.51$ ). A linear regression analysis was carried out to test the assumption of a linear relationship between distance and capture time. The analysis gave a significant result only for the low temperature (T=14°C,  $F_{1,19}=5.1$ ,  $p=0.04$ ; T=21°C,

$F_{1,19}=2.3$ ,  $p=0.14$ ; T=27°C,  $F_{1,19}=3.1$ ,  $p=0.09$ ). However, considering that all  $F$ -values are relatively high and the number of replicates is relatively low, it is justifiable to proceed with calculating the capture speed assuming a linear relationship between distance and capture time for all three temperatures.

There was a significant difference in the reaction time of *Araneus diadematus* to incoming prey at the three temperatures tested (MANOVA  $F_{2,19}=6.96$ ,  $p=0.0054$ ). It is evident from Fig. 2A that the reaction time at the lowest temperature was significantly longer than at the two higher temperatures; moreover it also showed much higher variability. The time interval between impact of the fly and the first reaction of the spider was more than twice as long at 14°C as at the two higher temperatures.

The same trend was found for orientation time (Fig. 2B), although here the differences were not significant (MANOVA  $F_{2,19}=3.10$ ,  $p=0.068$ ). As for reaction time,

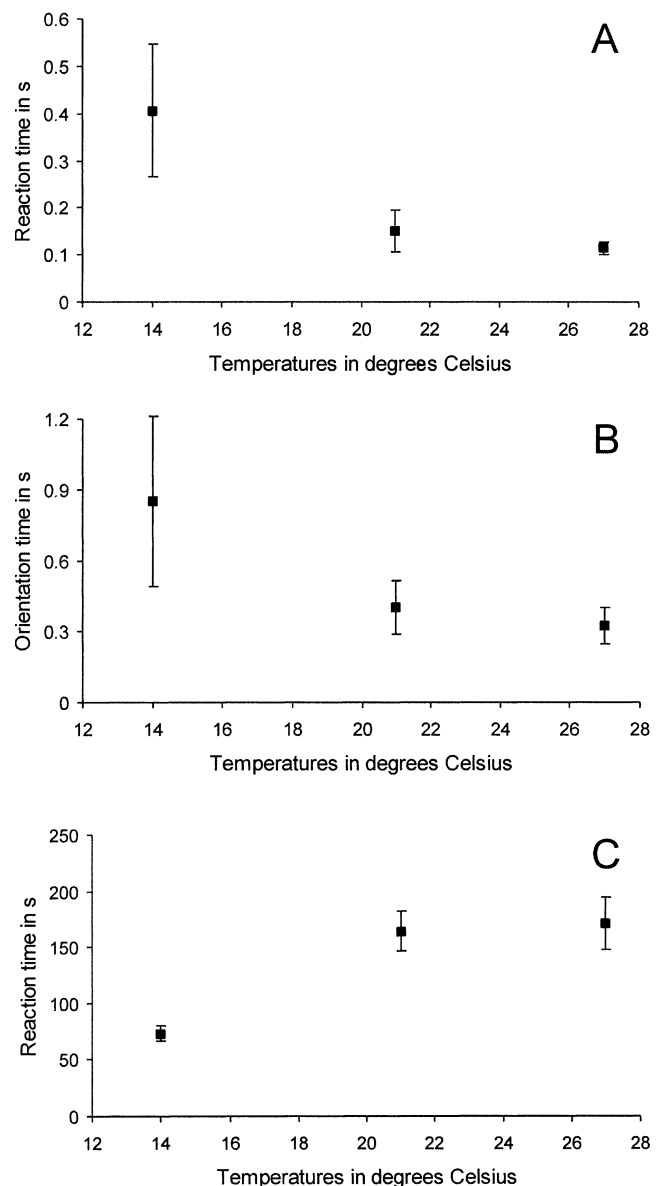


Fig. 2: Predatory behaviour of *Araneus diadematus* preying on *Drosophila melanogaster* at different temperatures (14, 21 and 27°C). Each data point is based on 21 predatory events. **A** Mean reaction time in s; **B** Mean orientation time in s; **C** Mean capture speed in mm/s. Error bars indicate SE.



the orientation time was more than twice as long at 14°C compared with at 21°C and 27°C, and again was more variable.

Capture speed increased with temperature as shown in Fig. 2C (MANOVA  $F_{2,19}=20.74$ ,  $p<0.0001$ ). The speed at which the spider rushed out to seize the prey at 14°C was less than half that seen at the higher temperatures. As the three graphs in Fig. 2 indicate, the observed effect of temperature on prey-capture success was additive: at lower temperatures the spider took longer to react, longer to orient, and was slower once on its way. The differences between the two higher temperatures were not significant, although at the highest temperature the spiders were marginally faster for all three aspects of predatory behaviour tested here.

Bringing together the results of the experiment on fly escape time and the experiment on capture speed allows us to estimate the capture efficiency for the three temperatures tested. The proportion of fruit flies caught was calculated to be around 70% for the two lowest temperatures, whereas it dropped to around 60% at the highest temperature (Table 1). This gives a fly an average difference in capture probability that is 10% lower at the highest temperature.

## Discussion

Our study showed that temperature has a significant impact on the dynamics of the orb-weaver predator–prey interaction. Increasing temperatures resulted in faster dynamics, both for the escape time of the flies from the web and for the reaction time of the spider.

It is highly unlikely that temperature (in the range tested) affects the stickiness of the capture thread (Vollrath, unpubl. obs.). Thus it seems most likely that the observed temperature dependence of fly escape time is related primarily to fly activity. This explanation agrees with the findings of other studies on the relation between temperature and activity level in *Drosophila melanogaster* (Sewell, 1979) where muscle mechanical power in *D. melanogaster* increases with increasing temperatures from 5–30°C (Lehmann, 1999). This explanation would further agree with Nentwig's (1982) hypothesis that increased activity (i.e. wriggling) of captured prey leads to faster escape times.

Not only did the flies escape more quickly at higher temperatures, but elevated temperatures also affected the spider by speeding up its reaction time, its prey-

orientation and its running speed. The spider detects and localises the intercepted fly through thread-transmission of its vibrations (Landolfa & Barth, 1996; Masters *et al.*, 1986), and more strongly struggling flies would create stronger signals leading to increased (and faster) reaction. However, even if this were to affect the reaction/orientation time, we are inclined to attribute the significant temperature dependence of spider running speeds to a direct correlation with increased muscle power, comparable to Lehmann's (1999) *Drosophila* study. It is also known that web-building speeds in spiders are strongly correlated with temperature (Vollrath *et al.*, 2001).

The results on predatory behaviour obtained in this study agree with those from earlier studies. None of these studies was explicit about the experimental temperatures which, however, seemed to be ambient. Ap Rhisiart and Vollrath (1994) report that immature *Araneus diadematus* preying on *Locusta migratoria* (length  $\approx 10$  mm) show a reaction time of  $0.41 \pm 0.36$  s, an orientation time of  $0.49 \pm 0.40$  s and a capture speed of  $164.4 \pm 14.5$  mm/s. The last two variables agree very well with the results presented here, but in our experiments the reaction time was significantly shorter. This can probably be explained by the difference in prey species or the different way of presenting the prey into the web. Detection of prey depends on the initial activity of the prey (Suter, 1978), which again is species dependent (Nentwig, 1982). In the study presented here, care was taken to handle the fruit flies carefully in order to ensure that they actively tried to free themselves upon entanglement.

Our study indicates that there is a pronounced effect of temperature on both the prey's escape time and *Araneus diadematus*' catching time. However, whereas fly escape time was nearly linear with temperature (as can be inferred from Fig. 1), spider behaviour was not but instead clearly levelled out for all three variables at the higher temperatures. Might this suggest that the "optimal" temperature for a spider's prey capture behaviour lies between 14 and 21°C?

In Denmark, the home of our spiders, *A. diadematus* is active from April to October (pers. obs.). During this period it encounters a wide range of temperatures. According to the Danish Meteorological Institute, in the coldest month, April, the average day temperature is 9.6°C (max. for 2002 was 23°C) and the average night temperature is 2.1°C (min. for 2002 was  $-5$ °C). In the

Temperature	Catching time <sup>a</sup>	Conf. Interval <sup>b</sup>	Prop. Caught <sup>c</sup>	Conf. Interval <sup>d</sup>
14°C	2.38 s	1.29–3.47 s	69%	60–82%
21°C	1.20 s	0.74–1.66 s	71%	63–78%
27°C	1.14 s	0.72–1.56 s	61%	50–75%

Table 1: Total catching time and the corresponding capture success for *Araneus diadematus* preying on intercepted *Drosophila melanogaster*. a=catching time calculated from capture speed, with constant distance set at 60 mm, added to reaction time and orientation time for each of the 21 samples at each temperature; b=95% confidence interval on catching time; c=proportion caught=percentage of flies still retained in the web at the given temperature, when the catching time has elapsed; these values taken from Fig. 1; d=confidence interval of proportion caught, found by reading the extremes of the confidence interval at the catching time, derived from Fig. 1.

warmest month, August, the average day temperature is 20.0°C (max. for 2002 was 32°C) and the average night temperature is 11.3°C (min. for 2002 was 8°C). If we are correct in our hypothesis of adaptive capture speeds, then spiders originating in warmer climes should have different reaction-time curves from our Danish spiders if the escape time of local prey is even faster at higher temperatures. We note that the flies we used originated from the genetics laboratory and were not locally adapted.

Activity in prey insects, as with all poikilothermic animals, depends on the ambient temperature (Rott & Ponsonby, 2000; Lehmann, 1999; Sewell, 1979; Precht *et al.*, 1973) or rather, more specifically, on body temperature, which depends on insect size (Merrick & Smith, 2004; Lactin & Johnson, 1998), activity (Merrick & Smith, 2004) and insulation (Merrick & Smith, 2004). Clearly, other prey species will differ from *Drosophila*, e.g. the honey bee, *Apis mellifera*, maintains a thoracic temperature 10°C above ambient temperature (Roberts & Harrison, 1999). Such an animal could maintain its optimal escape speed even on a cold morning or evening while the spider has a lower capture speed, probably allowing the bee to escape more often than not. However, prey capture in web spiders depends not only on reaction speeds at the time of capture, but also on behaviour sequences executed hours earlier. The web is an integral part of the prey capture behaviour and, interestingly, web geometry is also affected by temperature at the time of building (Vollrath *et al.*, 1997). Thus, it seems probable that the spider's prey capture behaviour is more complex than at first thought. Does the spider build a "cheaper" web (less dense with higher escape probability) when high temperatures are expected for the peak prey capture periods and a more expensive web (denser with more sticky threads) when low temperatures are expected? Spiders like *Araneus* certainly are able to adapt their webs to their expected prey (Sherman, 1994; Schneider & Vollrath, 1998) and appear to be able to predict changes in the weather (Quatremere-Disjonval, 1792), perhaps using barometric pressure as a proximate cue (Wolff & Hempel, 1951). However this may be, our study has shown that it would be profitable to investigate in more detail the interactive effects of temperature on spider and prey, and the influence of web geometry on the temperature-dependent predator-prey dynamics since this should have important implications for the evolutionary arms race between spider and fly.

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