

The effect of temperature on phototactic behaviour in *Celaenia kinbergi* Thorell, 1868 (Araneae: Araneidae)

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Summary

A new form of light-orientated behaviour in newly-emerged *Celaenia kinbergi* spiderlings has been found. With increasing light intensity, the animals crawl more rapidly and more directly towards the light. The behaviour is most evident from 28 to 35°C. The behaviour may be advantageous to the species by increasing the efficiency of ballooning behaviour exhibited by newly-hatched spiderlings of this species.

Introduction

During other studies it was observed that spiderlings reared in clear vials aggregated on the side facing the light. The following experiments were designed to investigate this behaviour further. Newly-emerged spiderlings of *Celaenia kinbergi* Thorell, 1868, known locally as the bird-dung spider, were used.

Descriptions of light-orientated behaviour patterns in spiders are rare in comparison with those of many other groups of animals as diverse as amoebae (Manwell, 1968), insects (Jander, 1963), crustaceans (Hardy, 1970), reptiles (Carr, 1965) and birds (Matthews, 1968; Griffin, 1974; Emlen & Penney, 1966). Cloudsley-Thompson (1978) in his review article, cites only Papi and his co-workers (Papi & Syrjamaki, 1963; Papi & Tongiorgi, 1963) as relevant to spiders. De Berre (1979) observed a general increase in locomotor activity in newly-emerged spiderlings of *Araneus cornutus* Clerck during daylight, while nocturnal activity appeared only after the second ecdysis.

Methods

Celaenia kinbergi egg sacs, collected in the field or laid in captivity, were broken open within an hour of the normal emergence of the first spiderling. All animals from each egg sac were counted and placed in a clear plastic container 10 × 10 × 12 cm. Moisture, but no food, was provided and each container was put in a continuously artificially lit room. Temperature was not controlled during rearing and varied between 26 and 33°C. Experiments were carried out 2 days after emergence.

The experimental apparatus consisted of a 60 watt pearl bulb in a 15 × 15 × 20 cm box with a 2 cm wide by 5 cm high slit on one side. Light intensity was controlled by a dimmer switch connected in series, and measured with a photometer. A perspex container 1 cm wide, filled with water and placed in front of the slit,

acted as a heat shield. The temperature range to which the animals were exposed was less than 1°C.

The apparatus was placed on a horizontal sheet of cream matt paper, 1.0 × 0.75 m, in a darkened, constant-temperature room. After every trial the sheet was wiped clean of any gossamer or trailing threads, and a new piece of paper was used after every 5 trials. If the sheet was not cleaned or replaced, spiderlings in later trials either followed the trailing threads or became entangled in the floating gossamer. After each trial the positions of the release point and the light source were altered; thus no pheromone trails could be left between them.

For each trial a release point 50 cm from the light source was selected, and light intensity was measured at this point. A 5 ml clear plastic vial containing a single spiderling was placed on the release point. After a period of inactivity, ranging from a few seconds to several minutes, the spider crawled to the top of the tube and down onto the paper. The position at which the animal emerged from the vial had no apparent effect on the direction in which the animal moved after leaving the vial. Timing of the trial began when the spiderling had crawled 2 cm from the release point. After 60 seconds, (i) the net distance travelled from the release point, and (ii) the angle of deviation of the final point from a straight line drawn between the release point and the light source, were measured. The spiderling was not touched at any stage of the trial. After the trial the spiderling was returned to another holding container with other spiderlings from the same egg sac. An individual was used only once in any set of trials.

The angles of deviation (as defined above) were grouped into 6 sectors of 60° each. Sector 1 was defined as being from 1-30° or 331-360°, sector 2a from 31-60° or 301-330°, sector 2b from 61-90° or 271-300°, sector 2c from 91-120° or 241-270°, sector 2d from 121-150° or 211-240°, and sector 2e from 151-210°.

Results

The effects of light intensity

Spiderlings from 2 egg sacs, laid by different mothers, but which hatched simultaneously, were used for this experiment. Fifty spiderlings were drawn from each egg sac. Each animal was run in 3 trials, at 6, then 3 and finally 9 lux. Successive trials for an animal were separated by at least 45 minutes. A smaller group of 20 trials was attempted at zero lux, but over a period of 7 minutes none of the spiderlings attempted to crawl out of the vial at the release point.

Plotting light intensities over the experimental field showed a geometric decrease along the field moving away from the light source and a gaussian distribution across the field with the maximum intensity directly in front of the slit. This pattern was observed for all light intensities used. Experiments were conducted between 2230 and 0300 h. The ambient temperature and humidity, monitored with a thermohydrograph, remained constant in the dark room throughout this period.

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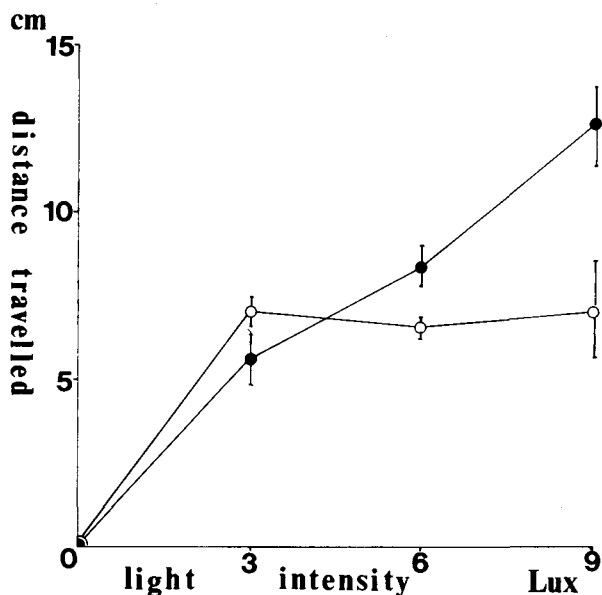


Fig. 1: The effect of light intensity on the mean distance travelled (in cm) by spiderlings in 60 seconds. Solid circles = spiderlings that walked directly towards the light (Sector 1). Open circles = spiderlings that did not walk directly towards the light (Sectors 2a-e). Bars represent S.E.

In the trials the animals were divided into 2 groups on the basis of whether they walked directly towards the light (sector 1) or did not (sectors 2a-e). The mean distances travelled were calculated for each group, and are plotted against the light intensity (at the point of release) in Fig. 1. For each group the hypothesis that the mean distance travelled is a function of light intensity was tested for regression. For the group in sector 1 the slope of the regression was 1.4 cm/lux.

However, for the animals that did not walk directly towards the light the slope was almost zero, implying that, unlike the group in sector 1, an increase in light intensity did not result in an increase in distance travelled. At 3 lux, a *t*-test indicated no significant difference between the 2 groups in the mean distance travelled. As the animals placed at the release point in complete darkness did not move, they obviously have a threshold for activity somewhere between zero and 3 lux.

Plotting the frequency distribution of the animals' final position within the 6 sectors (Fig. 2) indicates that at 6 and 9 lux most of the animals ran directly towards the light source but at 3 lux a smaller number ran towards the light source and a significantly ($p < 0.05$) larger number ran in sector 2.

It is evident from these results that there is a significant tendency for *Celaenia* spiderlings to run towards the light. Furthermore, this behaviour is more pronounced, in terms of both the proportion of spiders running directly towards the light and the net distance travelled in a given time, at higher light intensities. The trend is to orientate and move directly towards the light, rather than at an angle to the light as a light compass response.

The effect of temperature

A group of 50 animals was taken from each of 5

different egg sacs laid by 5 different females. Results from the 5 groups of animals were pooled. Constant temperatures of 20, 28, 35 and $37 \pm 0.5^\circ\text{C}$ were maintained in constant-temperature rooms. Each animal was given 30-60 minutes to equilibrate at each temperature before being given a run in the apparatus using a light intensity of 9 lux at the point of release. Each animal was run once at each temperature. The runs were conducted between 1400 and 1800 h.

A relationship between the phototactic response and temperature was observed. The relationship between distance travelled and the temperature for animals travelling towards the light (sector 1) and also those travelling in other directions (sectors 2a-e) is shown in Fig. 3. A similar relationship was observed in both groups, and no statistical difference was found between the 2 groups at any temperature.

For both groups there was (i) a significant increase in the distance travelled between 20 and 28°C , (ii) no difference between 28 and 35°C , where the spiders appeared to move at their maximum rate, and (iii) a significant decrease between 35 and 37°C .

The distribution between sectors, of animals after they finish their runs, is shown in Fig. 4. The number of animals running directly towards the light (sector 1) at 35°C is significantly greater ($p < 0.025$) than at either 20 or 37°C .

The statistical differences between the mean distances travelled are related to other observed differences in behaviour at the different temperatures. At 28 and 35°C the spiderlings quickly leave the area immediately surrounding the vial. Having done so, they run with few stops, often leaving drag-lines attached to

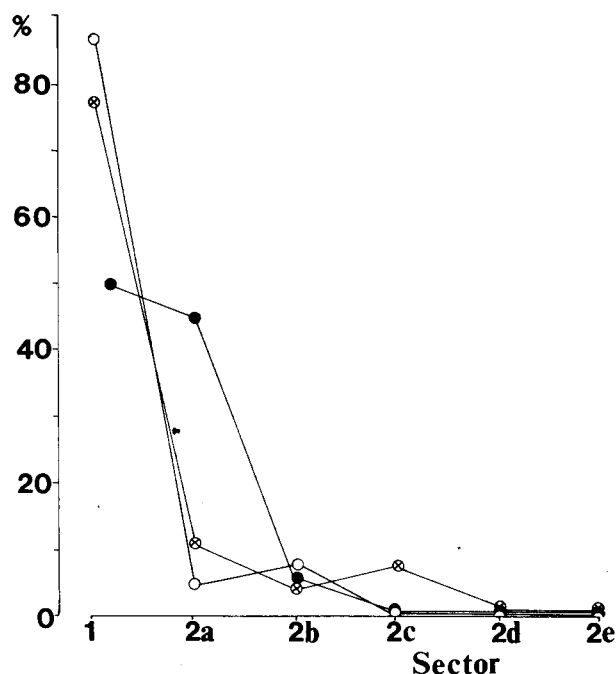


Fig. 2: The effect of light intensity on the final positions of spiderlings after 60 seconds, as measured by the angle of deviation from a straight line between the point of release and the light source, expressed as percentage of spiderlings in each sector. For details of sectors see text. Solid circles = 3 lux, cross-hatched circles = 6 lux, open circles = 9 lux.

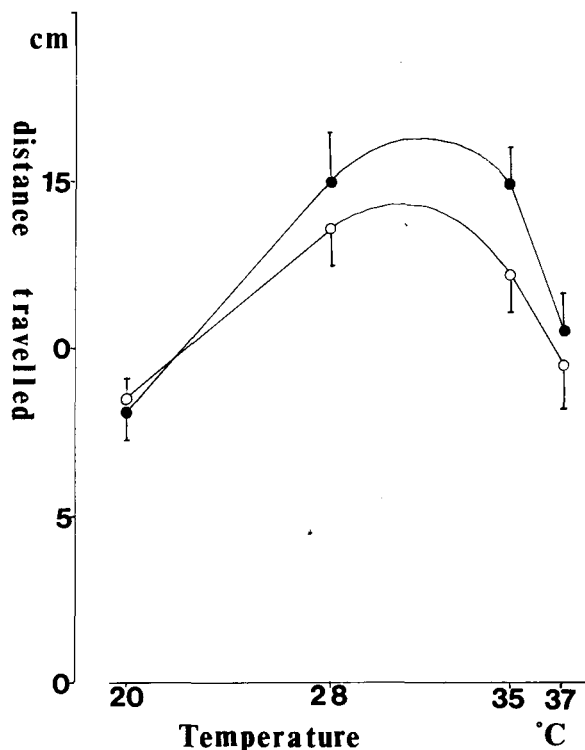


Fig. 3: The effect of temperature on mean distance travelled (in cm) at a light intensity of 9 lux by spiderlings that ended their runs in Sector 1 (solid circles) or in Sectors 2a-e (open circles). Bars represent S.E.

the sheet of paper. By comparison, at 20°C, the animals are lethargic, slow in starting, and their course after leaving the vicinity of the vial is slow and tortuous. At 37°C, they spend a great deal of time motionless. At this high temperature very few drag-lines are spun out, but almost all spiderlings let out copious quantities of ballooning thread. As the ballooning thread is released the spiderlings adopt the position described by Bristowe (1939: 61) and remain motionless.

Discussion

The results show a clear positive phototactic behaviour in the sense used by Oldroyd (1968), i.e. "a movement governed by light intensity in which the animal moves toward the greater intensity, as opposed to a light compass reaction where the animal moves at an angle to the light." The phototaxis observed is not dependent on a temperature gradient within the experimental apparatus, but the rate of movement towards the light is affected by the temperature and is greatest between 28 and 35°C. The proportion of animals which elicit the response is also greatest between 28 and 35°C.

While no evidence of photonegative behaviour was observed, the results may be compared with the light compass behaviour of certain insects (Sullivan & Wellington, 1953; Wellington, 1960; Wellington, Sullivan & Green, 1951) which show a photopositive response at low temperatures and a photonegative response at high temperatures. In these insects it was proposed that the behaviour would be beneficial for the

species in reducing dehydration by limiting dispersal to occasions when temperatures outside the microhabitat were suitable.

The evidence presented here fits well with other observations on the behaviour of *Celaenia kinbergi* (Roberts, 1937; Main, 1976; McKeown, 1952) and on dispersal mechanisms in other spiders (Bristowe, 1929; Duffey, 1956; Meijer, 1977). It is also consistent with the finding that spiderlings before the second ecdysis show more motor activity during daylight hours (DeBerre, 1979) and that ballooning occurs in *Pardosa* spiderlings on warm days (Richter, 1970).

The behaviour described here, which may be observed at any time of the day or night, would undoubtedly facilitate dispersal on the warm days which are appropriate for ballooning. The egg sacs of *Celaenia* are invariably found in the shaded inner regions of shrubs or bushy trees. After hatching at the beginning of a warm day, the spiderlings would be drawn in the direction of greatest light intensity, which would normally be towards the outside and upper parts of the plant. This position would pose the fewest obstacles for the spiderling when it began ballooning, enhancing the efficiency of the ballooning behaviour for dispersal. When the weather is cool, and so inappropriate for ballooning (Richter, 1970), the spiders become inactive.

Furthermore, the ambient temperature would be several degrees lower in the leafy shade of the bush compared with the leaves exposed to the sun on the outside of the bush. Under these conditions the change in activity from a photopositive behaviour to a ballooning behaviour in the temperature range 35 to 37°C, as observed in the laboratory, could be expected.

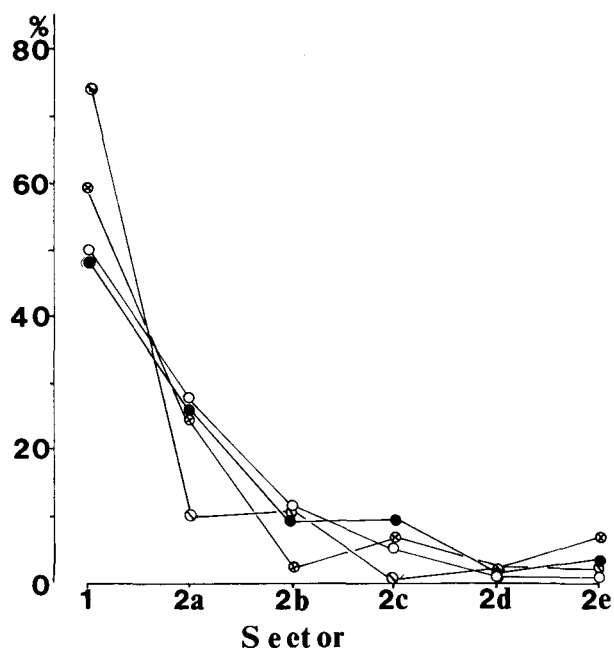


Fig. 4: The effect of temperature on angle of deviation from a straight line between the point of release and the light source, at a light intensity of 9 lux, expressed as percentage of spiderlings in each sector after 60 seconds. For details of sectors see text. Solid circles = 20°C, open circles = 37°C, cross-hatched circles = 28°C, hatched circles = 35°C.

The author has observed the proposed sequence in the field by placing spiderlings from a number of egg sacs on the interior, shaded leaves of citrus trees at a height of 1 m. On days when the temperature ranged from 28 to 35°C in the shade, the animals quickly made their way to the outer, upper parts of the plant. Two hours after release, none were found below 2 m from the ground, and some had reached 3 m: almost all were in the outermost branches. The following morning not one animal could be found on the trees. On colder days when the shade temperature did not rise above 20°C, some spiderlings could be found on the tree 48 hours after release, often in the same position in which they had been released.

Since the proposed sequence of behaviour is a simple yet effective preliminary to dispersal by ballooning, it is likely to be found in many other species of spider which disperse by ballooning.

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References

- BRISTOWE, W. S. 1929: The distribution and dispersal of spiders. *Proc.zool.Soc.Lond.* **1929**: 633-657.
- BRISTOWE, W. S. 1939: *The comity of spiders* 1: 1-228. London, Ray Society.
- CARR, A. 1965: Navigation of the green turtle. *Scient.Am.* **212**: 79-86.
- CLOUDSLEY-THOMPSON, J. L. 1978: Biological clocks in Arachnida. *Bull.Br.arachnol.Soc.* **4**: 184-190.
- DE BERRE, M. 1979: Mise en place du rythme d'activité chez *Araneus cornutus*. *C.r.hebd.Séanc.Acad.Sci., Paris* (Ser. D) **288**: 839-842.
- DUFFEY, E. 1956: Aerial dispersal in a known spider population. *J.Anim.Ecol.* **25**: 85-111.
- EMLEN, J. T. & PENNEY, R. L. 1966: The navigation of penguins. *Scient.Am.* **215**: 104-113.
- GRIFFIN, D. R. 1974: *Bird migration*. New York, Dover.
- HARDY, A. 1970: *The open ocean*. Boston, Houghton.
- JANDER, R. 1963: Insect orientation. *A.Rev.Ent.* **8**: 95-114.
- MAIN, B. Y. 1976: *Spiders*. Sydney, Collins.
- MANWELL, R. D. 1968: *Introduction to protozoology*. New York, Dover.
- MATTHEWS, G. V. T. 1968: *Bird navigation*. Cambridge, Cambridge University Press.
- McKEOWN, K. C. 1952: *Australian spiders* (2nd Ed.). Sydney, Angus & Robertson.
- MEIJER, J. 1977: The immigration of spiders into a new polder. *Ecol.Entomol.* **2**: 81-90.
- OLDROYD, H. 1968: *Elements of entomology*. New York, Universe.
- PAPI, F. & SYRJAMAKI, J. 1963: The sun orientation rhythm of wolf spiders at different latitudes. *Archs ital.Biol.* **101**: 59-77.
- PAPI, F. & TONGIORGI, P. 1963: Innate and learned components in the astronomical orientation of wolf spiders. *Ergebn.Biol.* **26**: 259-280.
- RICHTER, C. J. J. 1970: Aerial dispersal in relation to habitat in eight wolf spider species. *Oecologia (Berl.)* **5**: 200-214.
- ROBERTS, N. L. 1937: Some notes on the bird dung spider. *Proc.R.zool.Soc.N.S.W.* **1936-37**: 24-28.
- SULLIVAN, C. R. & WELLINGTON, W. G. 1953: The light reactions of larvae of the tent caterpillars. *Can.Ent.* **85**: 297-310.
- WELLINGTON, W. G. 1960: The need for direct observation of behaviour in studies of temperature effects on light reactions. *Can.Ent.* **92**: 438-448.
- WELLINGTON, W. G., SULLIVAN, C. R. & GREEN, G. W. 1951: Polarized light and body temperature level as orientation factors in the light reactions of some hymenopterous and lepidopterous larvae. *Can.J.Zool.* **29**: 339-351.