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Jacob Blaustein Institute for Desert Research,  
Ben Gurion University of the Negev, Sede Boqer,  
and Desert Ecological Research Unit of Namibia, Swakopmund

## Experimental Evidence that a Desert Parasitoid Keeps its Host Cool

DAVID WARD & JOH R. HENSCHEL

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### Abstract

The wasp parasitoid *Pseudopompilus humboldti* (Hymenoptera; Pompilidae) in the Negev desert of Israel stores its paralyzed host, the spider *Stegodyphus lineatus* (Araneae; Eresidae), at the entrance of the spider's nest. The spider is moved by the wasp from the depth of the nest to the entrance in spite of increased exposure to visually-searching predators, such as birds. We examined the hypothesis that this behaviour has evolved to prevent the wasp's host from overheating in this hot desert. Experimental manipulations of the position of the parasitized spiders demonstrated that spiders and wasp larvae could not survive the heat experienced deep in the spider's nest during summer. By contrast, in the cooler nest entrance, spiders and larvae survived, if they were overlooked by predators. This host-storing behaviour is an adaptive trade-off between thermoregulatory requirements and predation risk. This appears to be the first evidence that a parasitoid manipulates the temperature of its host, albeit for its own ultimate gain.

Corresponding author: David WARD, Ecology Group, Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, B. C., V6T 1Z4, Canada.

### Introduction

Most emphasis in studies of insect parasitoids and their hosts has been placed on searching and ovipositing behaviour of the parasitoid and its effects on the population dynamics, distribution and dispersion of their hosts (e.g. HOLLING 1959; HASSELL 1978; HUBBARD & COOK 1978; VAN ALPHEN & GALLIS 1983; WAAGE & GREATHEAD 1986). Here we examine the hypothesis that, in the Negev desert of Israel, a parasitoid wasp *Pseudopompilus humboldti* manipulates the position of the paralyzed spider *Stegodyphus lineatus* that hosts its progeny in order to prevent the host and its larva from overheating. In doing so, the wasp ensures that its host remains alive so that it can be consumed by the wasp larva.

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**Natural history of the interaction:** In the Negev desert, *Stegodyphus lineatus* (Araneae; Eresidae) build tubular nests near the tops of dwarf shrubs (LEVY 1985). The nest is usually oriented with the entrance facing downwards. The capture web radiates from the mouth of the nest in a two-dimensional array of non-sticky, radial elements and sticky (cribellar) silk connecting threads (Fig. 1). The web has the appearance of an "untidy" orbweb and is designed to trap flying insects. The nest is made of very dense and "woolly" silk, with remains of prey (arthropod exoskeletons), snail shells and plant debris embedded in its walls.

The female parasitoid wasp *Pseudopompilus humboldti* (Hymenoptera; Pompilidae) flies on to the web near the attachment to the nest and vibrates its wings. This movement may imitate the vibrations caused by a captured flying insect and stimulates the spider to rush down from the top of its tubular nest towards the nest entrance. The parasitoid responds to the spider's movement by moving into the nest to meet the spider about halfway up the tube. The wasp then stings the spider to paralyze it. Thereafter, the wasp lays a single egg on the outer surface of the spider's opisthosoma (abdomen). The wasp then pushes the paralyzed spider to the nest entrance. The wasp abandons the nest after having placed the spider in the entrance tunnel. The egg hatches and develops through the larval and pupal stages in about two weeks.

We hypothesized that the above-mentioned manipulation of the spider's position by the wasp occurred in order to keep the spider from overheating in this hot desert. This happens in spite of the increased vulnerability to visual predators, such as birds, that this behaviour causes (WARD & LUBIN 1993). Based on previous measurements of *S. lineatus* nests (HENSCHER et al. 1992), we predicted that a parasitized spider would get too hot in the thick nest during the heat of the day. For the wasp larva to develop, the spider would need to be moved to the cooler nest entrance where it would be shaded from direct solar radiation and could cool convectively in the wind.

## Materials and Methods

**Study site:** The study site was located on Haluqim Ridge in the central Negev desert highlands, Israel, near the settlement of Midreshet Sede Boqer (30°52'N, 34°57'E, 475 m above sea level). The terrain consists of stony hillsides, with sparse dwarf shrubs (mostly *Artemisia herba-alba*, *Hammada scoparia* and *Zygophyllum dumosum*; EVENARI et al. 1982). The rainfall in this region is very low (85 mm per annum), falling in the winter months of Nov. through Jan. The Negev desert highlands are considered "arid", having 250 to 300 biologically dry days per annum and a precipitation: evaporation ratio of less than 0.2 (UNESCO 1977).

Average daily air temperature for the hottest (Jul.) and coldest (Jan.) months is 25.5 °C and 9.8 °C, respectively. The mean daily maximum temperature during the study period ranged from 19.8 °C (Mar.) to 33.2 °C (Jul.). The mean daily minimum temperature during this period ranges from 7.1 °C (Mar.) to 19.6 °C (Jul.). The annual average relative humidity at 14.00 h is 39 % (ZANGVIL & DRUIAN 1983).

**Population monitoring:** The incidence of parasitism of spiders by wasps was observed in a natural population in two study sites (8.5 and 4 ha in size) that were about 5 km apart. We monitored 105 and 54 spiders during the summers of 1989 and 1990, including their causes of death. Parasitism was recognizable from the spider's fixed position in the nest entrance and the presence of a wasp egg,

larva, or pupal cocoon on or next to a paralyzed or consumed spider. Predation by birds left nest entrances torn as evidence of such events.

**Experimental manipulation:** In order to determine whether the spider is pushed to the entrance of the nest to keep it and the larva cool, we performed the following manipulation in June 1990:

1. Treatment: We placed 6 parasitized spiders (with wasp larva) deep into their nests.

2. Control: We moved 6 parasitized spiders (with wasp larva) around in the entrance of their nests and returned them to the positions where the parasitoids originally placed them. This manipulation ensured that any difference between the experimental and control animals was not simply due to the effects of disturbance rather than changed position in the nest. At weekly intervals for one month, we re-examined all experimental and control animals to record their development.

**Temperature and wind measurements:** Simultaneous to the experiment mentioned above, temperatures in the nests and ambient temperature ( $T_a$ ) were measured using gauge 28 copper-constantan thermocouples. These thermocouples were calibrated against a mercury thermometer (approved by the United States National Bureau of Standards) with an error of  $\pm 0.1$  °C. One fine, gauge 34 thermocouple, connected to a Campbell model CR21X datalogger, was threaded through a fine syringe needle into the abdomen of a live parasitoid larva that was attached to the opisthosoma of a paralyzed spider. In addition, we measured air temperature in the nest at positions midway into and at the terminal end of the nest. Air temperature was measured with a thermocouple that had a small (3 mm diameter) gloss white (reflective) tip. This is the most accurate means of measuring air temperature in field studies (CHRISTIAN & TRACY 1985). This thermocouple was suspended from a wooden stick at the same height as the nest and 1 m from the nest entrance in an open area.

In order to corroborate our findings in the experimental nest that contained the wasp larva, we also measured the temperatures of aluminium model spiders of the same colour, size and shape as real spiders in six *S. lineatus* nests (HENSCHER et al. 1992). These temperatures represent operative temperature ( $T_o$ ) of a spider in various parts of the nest (BAKKEN 1976). The positions of the spider models and thermocouples in these other nests were the same as our measurements in the nest of a live, parasitized spider.

Temperatures were recorded every 5 s and averaged every 15 min. These averaged values were used because the time constant of the thermocouples is shorter than that of a spider and therefore each temperature measurement constitutes pseudo-replication. The averaged values were then used to compare temperatures of the parasitoid at the nest entrance with temperatures in the middle and deep in the tubular nest. Measurements were performed over two days and two nights.

The wind-speed profile near the nests was measured with Campbell model 03101-5 R.M. Young Wind Sentry anemometers. The wind-speed sensor consists of three hemispherical plastic cups (40 mm diameter) with a threshold sensitivity of 0.2 m/s stall speed. Wind-speed sensors were located 100, 50 and 25 cm above the substratum on a single pole about 2 m from the nest-shrub in an open area free of vegetation. Anemometers were calibrated in a wind tunnel using a Pitot tube and Airflow Developments Ltd. Type 5 manometer and EDM 2500M micromanometer. The dimensions of the wind tunnel are 700 mm diameter and height; total length 10.7 m; two-dimensional 7 : 1 contraction cone and axial flow fan (PYE & TSOAR 1990).

In order to determine whether spiders move into their nest entrances during the heat of the day under natural conditions, we recorded the position of 31 unparasitized spiders in the field. Spider position was recorded as either in the nest (not visible) or in the nest entrance. These records were taken every 2 h through an entire day. Air temperature was recorded simultaneous to these observations in the manner outlined above.

## Results

**Behavioural observations:** During 1990, 25.6 % of the spiders in natural populations ( $n = 54$ ) were parasitized. Another 18.5 % of the spiders were captured by birds in the nest entrances. No parasitized spiders were naturally found positioned deep inside the nest.

The entire behavioural sequence of the interaction between wasp and spider was observed on two occasions. On numerous other occasions, wasps were

observed alighting on the web but the complete sequence was terminated, probably as a result of accidental human disturbance. These observations were made during cool mornings, at a time when the adult female wasp could not test the maximum thermal gradient in the nest by direct experience.

Spiders appeared to respond to the vibrations of the wasp on the web. We tested this by vibrating the web with a musical tuning fork (440 Hz) in 255 tests. We were able to induce the same response as to a wasp, i.e. the spider rushed down the tubular nest from the top towards the entrance once the web was vibrated, in 73 % of the tests.

**Experimental manipulation:** One week after the manipulation, all 6 experimental spiders that were placed inside the nests were dead. The spiders were shrivelled up, a symptom of desiccation in these soft-bodied arthropods. 4 of 6 control spiders (at nest entrances) survived to pupation; the remaining 2 fell prey to birds and ants.

**Temperature and wind measurements:** The temperature of the wasp larva was lower than the thermocouples in the middle and deep end of the nest during virtually all daylight hours (Fig. 2). At the highest air temperatures recorded (12.00–15.00 h), the larva was almost 15 °C cooler than the thermocouple deep in the nest. During this period, 81 % of the unparasitized spiders observed in the field ( $n = 31$ ) were in their nest entrances. Whereas 60 % of the individuals were deep in the nest at 6.00 h, only 19 % were in this position at 11.00 and 14.00 h;

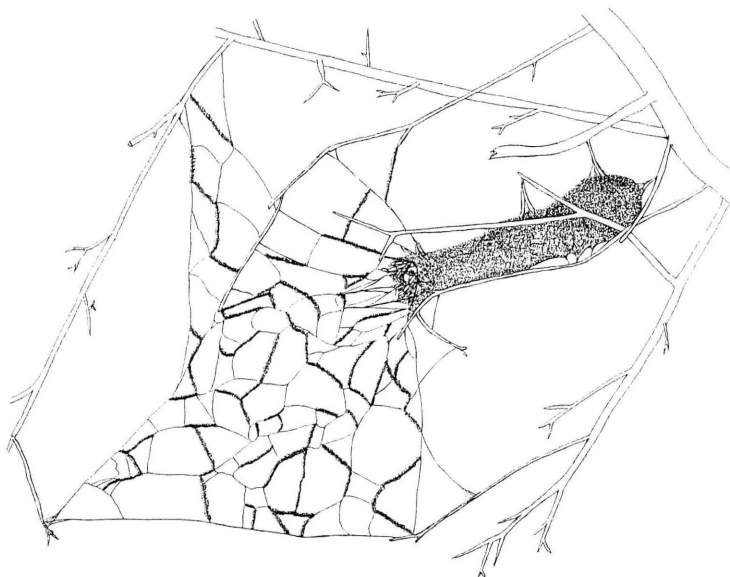


Fig. 1: Nest and capture web of *Stegodyphus lineatus*

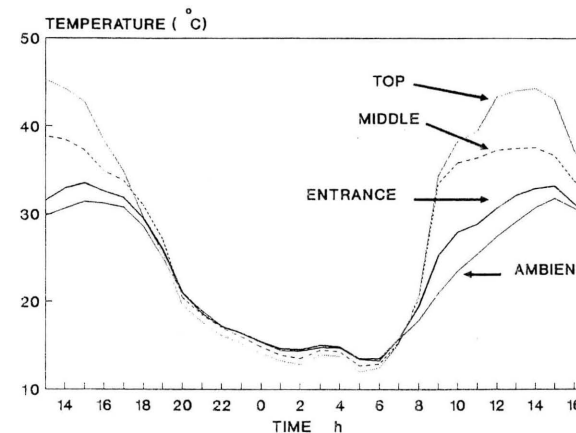


Fig. 2: Temperature profile in a nest of *Stegodyphus lineatus*: temperature of wasp larva in nest entrance, ambient temperature, temperature in the middle of the nest, and inside the top of the nest

the remaining 81 % had moved to the entrance where they are more vulnerable to predation (WARD & LUBIN 1992). Simultaneous temperature measurements in one nest indicated that at 6.00 h temperatures deep in the nest and at the nest entrance were 17.0 °C, while at 11.00 h these temperatures were 39.2 °C and 35.9 °C, respectively.

In the 6 nests containing spider models,  $T_c$  of the models in the nest entrances never exceeded 41 °C, the maxima being  $6.0 \pm 0.8$  °C (range =

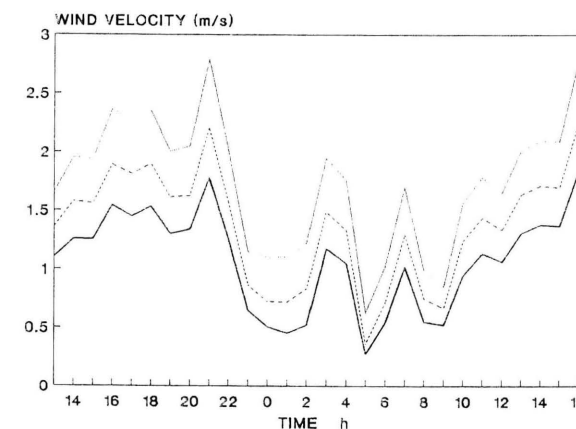


Fig. 3: Wind velocity profile near a parasitized nest. Wind velocities at different heights above the substratum are indicated by: bold line = 25 cm; dashed line = 50 cm; dotted line = 1 m

3.3–8.9 °C) lower than  $T_c$  of models deep in the nests (range = 43.9–49.5 °C).

A slight wind, although variable in its intensity, blows throughout the day and night in the Negev desert in summer (Fig. 3).  $\bar{X} \pm SE$  for the wind velocity at 25 cm above the substratum (the height of the nest) was  $1.10 \pm 0.08$  m/s (range = 1.84–0.27 m/s) during the study period. Such wind is sufficient to facilitate convective cooling of a small animal, such as this spider (CAMPBELL 1977). This accounts for the lower temperature in the wind-exposed entrance compared to the wind-sheltered inside of the nest.

### Discussion

Observations of wasps positioning paralyzed spiders in relation to expected tolerable temperatures are consistent with our hypothesis. An alternative hypothesis to explain the wasp behaviour is that wasps push the spiders to the nest entrances in order to indicate which spiders have been parasitized to save themselves search time on later excursions. We consider this improbable because:

1. This behaviour would also save time for competing parasitoids, increasing intraspecific competition for hosts.

2. Spiders in nest entrances are exposed to visually-searching predators such as great grey shrikes *Lanius excubitor* and Arabian babblers *Turdoides squamiceps* (KÖNIGSWALD et al. 1990; pers. obs.). Thus, the wasp increases the likelihood of detection by these predators. KÖNIGSWALD et al. (1990) examined the searching and prey-capture behaviour of great grey shrikes preying on the desert widow spider *Latrodectus revivensis* in the same habitat as the current study. The widow spider has a conical nest, covered with prey remains and plant debris, similar to that of *S. lineatus*. The shrikes did not capture any spiders that they could not detect visually.

We consider it probable, therefore, that the parasitoid behaviour has a thermoregulatory function for parasitized *S. lineatus*. This hypothesis is supported by the data presented here because:

1. Paralyzed spiders and their parasitoids died when we moved them deep into the nests; only those parasitoid larvae that were on spiders at the nest entrances eventually reached adulthood.

2. Premature death of paralyzed spiders in the nest was probably caused by overheating because: a) temperatures deep in the nest were 15 °C higher than at its entrance in the heat of the day; b) non-paralyzed spiders moved into the nest entrances during hot periods. It is likely that this behaviour occurs in order to facilitate convective cooling (HENSCHER et al. 1992).

The spider-manipulation behaviour of *P. humboldti* is unusual because many other species of parasitoid wasps go to great lengths to hide their hosts to avoid multiple or hyper-parasitism (e.g. EVANS 1953; WAAGE & GREATHEAD 1986; HENSCHER 1990). Indeed, members of the Pompilidae usually take the parasitized spider and store it in a cell made of mud (EVANS 1953). A few pompilid species have been recorded storing spiders in plant material, but this appears to be only a

temporary measure while a mud cell is being dug (PECKHAM & PECKHAM 1898; KROMBEIN 1953). We presume that, because free water is not available in this desert in summer, making a mud cell is not an option available to these wasps.

Other species of *Stegodyphus* also appear to experience frequent wasp parasitism. EL-HENNAWY (1986) recorded 19.3 % parasitism of *Stegodyphus dufouri* by *P. humboldti* in Egypt. MEIKLE-GRISWOLD (1986) observed high rates of parasitism of *S. mimosarum* and *S. dunicola* in South Africa. Parasitoids of other spider species may also place their immobile hosts into thermally-favourable environments. An incidental observation by HENSCHER (unpubl.) of a wasp-parasitized *S. dunicola* positioned at the nest entrance on the periphery of the Namib desert, Namibia, suggests that this behaviour might be more widespread in deserts than is currently realized.

It is evident that the behaviour of the parasitoid described here has evolved through natural selection to prevent the host from overheating. This behaviour may be considered proximate thermoregulation and a form of parental care by the wasp.

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