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Activity pattern and thermal biology of a day-flying hawkmoth (*Macroglossum stellatarum*) under Mediterranean summer conditions

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Abstract. 1. The daily activity pattern and aspects of the thermal biology are described for the day-flying hawkmoth, *Macroglossum stellatarum* L. (Lepidoptera: Sphingidae), while foraging at a flowering population of *Lavandula latifolia* (Labiatae) under the dry-hot summer conditions of a southeastern Spanish locality.

2. The average abundance of *M.stellatarum* remained fairly constant from sunrise to about 17.00 hours (GMT), and a distinct peak occurred in the evening (18.00–20.00 hours).

3. Foraging took place over a broad range of microclimatic conditions, as described by air temperature (T_a; range 19–36°C) and solar radiation (IR; range 1–1025 Wm^{-2}).

4. The thoracic temperature (T_{th}) of insects remained within relatively narrow limits (39–46°C), with the highest values occurring around noon. Variation in T_{th} mainly reflected differences in T_a between foraging sites and times. T_{th} was nonlinearly related to T_a, the rate of increase of T_{th} with T_a decreasing with increasing T_a.

5. The unusual tolerance of high T_{th} exhibited by *M.stellatarum*, and its enhanced thermoregulatory capacity at high T_a, enable this species to withstand the severe environmental conditions faced during diurnal foraging in the Mediterranean summer.

Key words. Activity pattern, *Macroglossum stellatarum*, Sphingidae, thermal biology.

Introduction

Most hawkmoths (Lepidoptera: Sphingidae) are crepuscular or nocturnal, but species in the genus *Macroglossum* are characterized by their diurnal habits. In southern Spain, *M.stellatarum* L. forages by day even during the dry-hot summer characteristic of the Mediterranean-type climate. Hawkmoths have a very active metabolism, and produce large amounts of metabolic heat as a consequence of intense flight muscle activity (Casey, 1976, 1981). Given also their comparatively large body mass (around 0.30–0.40 g in *M.stellatarum*), diurnal hawkmoths foraging at high ambient temperature would be expected frequently to risk overheating, leading to a restriction of activity. For nocturnal hawkmoths, Heath & Adams (1965) speculated that overheating might restrict activity at air temperatures above 30°C. Here, the daily foraging pattern of *M.stellatarum* at a *Lavandula latifolia* Med. (Labiatae) flowering population is described in relation to its thermal biology. The thermal biology of hawkmoths has been studied in considerable detail (e.g. Dorsett, 1962; Heinrich, 1971a, b; Bartholomew & Heinrich, 1973; Bartholomew & Casey, 1978; Hegel & Casey, 1982), but these studies were generally conducted on nocturnal species under laboratory conditions. There have apparently been no previous investigations of the thermal biology of day-flying hawkmoths in the field.

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Methods

This study was conducted at a site in the Sierra de Cazorla (Jaén province, southeastern Spain) located at an elevation

of 1160 m (the 'Aguaderillos-1' site of Herrera; 1988, where further details may be found).

Data on activity patterns were obtained in the summers of 1982–87, as part of a more general study on the insect pollinator assemblage of *L.latifolia* (Herrera, 1987, 1988, 1989, 1990). The daily activity rhythm of floral visitors was assessed by counting the insects foraging at flowers at different times of day along a 80 m long transect crossing the plant population. Night observations at the start of the study did not provide evidence of nocturnal insect visitation (see Herrera, 1988, 1990, for further details on pollinator count methods). *M.stellatarum* foraged at *L.latifolia* flowers throughout the whole flowering period of the species (July–October; Herrera, 1988). For the purpose of this study, counts were grouped into 'early' (15 July to 15 August, 321 counts) and 'late' (16 August to 15 October, 184 counts) periods, and data from all years have been combined. Counts were grouped at hourly intervals for the analyses.

Measurements of insect thoracic temperature (T_{th}), air temperature (T_a) and incident radiation (IR) at the foraging site were performed for forty-four *M.stellatarum* individuals netted between 20 July and 20 August 1990 while they were foraging at *L.latifolia* flowers. For each of these, T_{th} was measured within 10 s of netting. All individuals netted had been in continuous flight for at least a few minutes prior to capture. To characterize the conditions of the foraging microhabitat, T_a and IR were measured within 1 min of capture at the site where the moth had been netted.

T_{th} was measured to the nearest 0.1°C using a fast-response (time constant 0.025 s) microprobe consisting of a copper–constantan thermocouple fitted inside a 0.33 mm external diameter needle (Hypodermic Needle Microprobe Type MT-29/1, Physitemp Instruments, Clifton, New Jersey), and a Type T Cole-Parmer Digital Thermocouple Thermometer. Readings were obtained by inserting the probe 3 mm into the moth's thorax. All moths handled flew off normally after probe insertion. IR and T_a were measured using, respectively, a Li-Cor LI-200SZ Pyranometer Sensor (spectral range 400–1100 nM) and a Li-Cor 1000–16 Air Temperature Sensor, connected simultaneously to a LI-1000 data logger (Li-Cor Inc., Lincoln, Nebraska). To standardize radiation measurements, all IR readings were made while holding the sensor's surface horizontal. Thus they refer to solar radiation intensity measured on the horizontal plane.

Throughout, means are reported ±1 SD, and N denotes sample size.

Results

The average abundance of *M.stellatarum* foragers remained fairly constant from sunrise to about 17.00 hours, and no distinct peak occurred over this period (Fig. 1). A sharp increase in activity took place in the evening (18.00–20.00 hours), when mean abundance became about 3–4 times higher than during the rest of the day. The daily activity pattern was essentially the same during the early (15 July to 15 August) and late (16 August to 15 October) periods (Fig. 1).

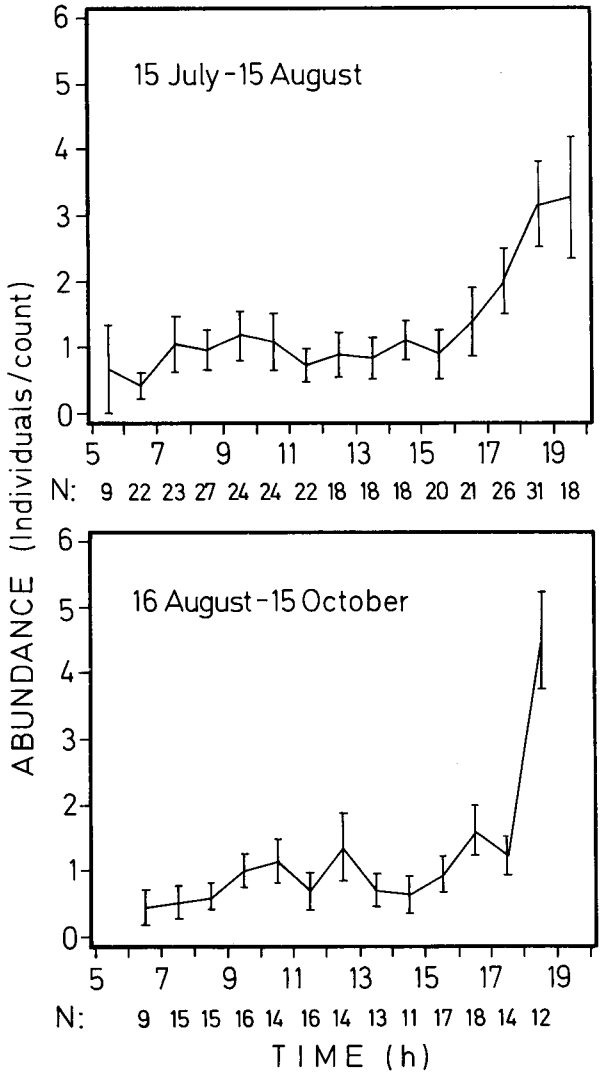

Fig. 1. Daily variation in mean abundance of *Macroglossum stellatarum* foraging at *Lavandula latifolia* flowers during 'early' (upper graph) and 'late' (lower graph) summer, years 1982–87 combined. Vertical bars extend ± SE around the mean. N, number of counts (sample size) in each hourly period.

As a consequence of its extended activity over daytime, *M.stellatarum* individuals foraged under a broad range of microclimatic conditions. Observed T_a and IR ranges (means in parentheses) for the sites of netted individuals were 19.4–35.9°C (26.2 ± 4.3°C) and 1–1025 Wm^{-2} (211 ± 335 Wm^{-2}), respectively ($N = 44$).

The observed range of hawkmoth T_{th} (mean in parentheses) was 38.6–45.8°C (42.7 ± 1.8°C). A distinct daily rhythm exists in T_{th} values (Fig. 2). T_{th} increased from 07.00 hours to 13.00 hours and then decreased from 16.00 hours to 19.00 hours (no hawkmoths were netted between 13.00 and 16.00 hours and a gap in the data exists for that

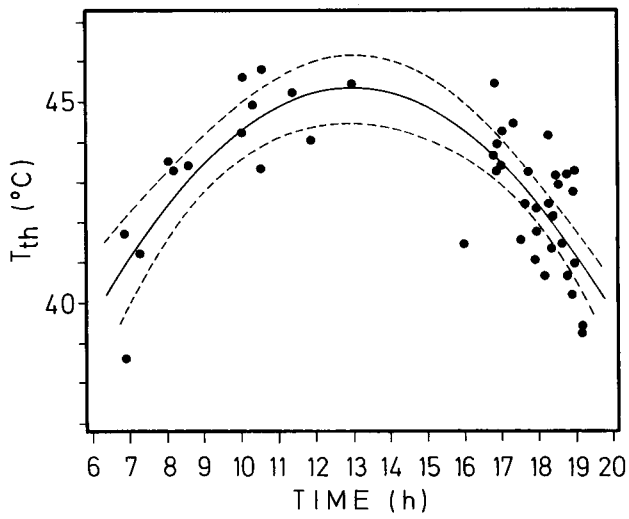

Fig. 2. Daily variation in thoracic temperature (T_{th}) of *Macroglossum stellatarum*. Dots represent individual measurements ($N = 44$), the continuous line is the fitted quadratic regression ($R^2 = 0.54$, $F = 24.0$, df = 2, 41, $P < 0.0001$), and dashed lines show the 95% confidence interval for the mean predicted values from regression.

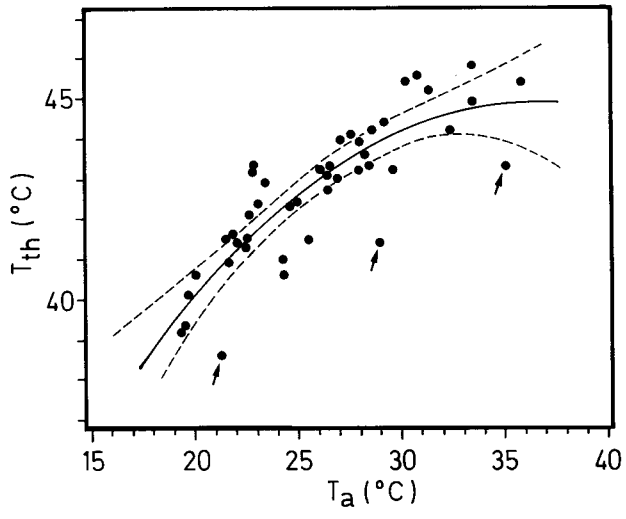

Fig. 3. Variation of thoracic temperature (T_{th}) with air temperature (T_a) in *Macroglossum stellatarum*. Dots represent individual measurements, the continuous line is the fitted quadratic regression ($T_{th} = 21.234 + 1.297T_a - 0.018T_a^2$), and dashed lines show the 95% confidence interval for the mean predicted values from regression. Two possible outliers and one data point with undue influence on the regression, are marked with arrows (see text).

period). The highest values (>45°C) were recorded in the periods 10.00–13.00 hours and 16.00–17.00 hours.

Daily variation in T_{th} presumably results from concomitant changes in T_a and IR, as these environmental variables largely determine temperature excesses in insects (May, 1979). A multiple linear regression was run using T_{th} as dependent variable and T_a and IR as independent ones. The regression equation was significant ($R^2 = 0.68$, $F = 43.3$, df = 2,41, $P < 0.0001$), but the two independent variables differed with respect to the significance of their respective regression coefficients. The coefficient for IR was not significantly different from zero ($t = 0.22$, $P = 0.83$), while that for T_a differed significantly ($t = 7.29$, $P < 0.0001$).

Adding a quadratic term to the linear regression equation of T_{th} against T_a improved significantly the accuracy of the prediction of T_{th} values ($F = 6.12$, df = 1, 41, $P = 0.017$). The fitted quadratic regression equation (Fig. 3) was highly significant ($F = 52.79$, df = 2, 41, $P < 0.0001$) and explained a substantial proportion of observed variance in T_{th} ($R^2 = 0.72$). The quadratic regression coefficient was still significant after removal of two presumed outliers and one point with undue influence on the regression (Fig. 3).

Discussion

On a yearly basis, *M.stellatarum* has been recorded visiting the flowers of at least twenty-six species of plants in the study area. In summer, however, foraging by this species is practically confined to *L.latifolia*, as it is virtually the only plant in flower during that period (C. M. Herrera, unpubl.). For this reason, daily variation in the abundance of *M.stellatarum* at *L.latifolia* flowers most likely reflects its rhythm of foraging activity during summer.

The average daily abundance profile of *M.stellatarum* was unrelated to the average daily rhythm of nectar availability exhibited by *L.latifolia* flowers, as its abundance peak occurred precisely when both the mean nectar volume per flower and the proportion of nectar-bearing flowers at the population were at their daily lowest values (Herrera, 1990).

The activity pattern of *M.stellatarum* was also apparently unrelated to weather conditions. Firstly, forager abundance remained remarkably constant for most of daytime, and increased sharply in the evening. This activity profile can hardly be explained by reference to the typical daily course of radiation and air temperature, both of which increase from sunrise to noon and decrease afterwards. And secondly, activity patterns were essentially the same for the 'early' and 'late' periods, even though these differ substantially in average weather conditions. This applies particularly to air temperatures, which tend to be predictably lower in the latter period. Monthly means of daily minimum–maximum temperatures for July, August, September and October at the nearest meteorological station (similar elevation, 4.5 km away), were 10.2–33.4°C, 10.6–31.8°C, 8.4–27.6°C and 5.0–20.7°C, respectively, in the 1982–87 study period. Furthermore, there is no evidence that the microclimatic conditions occurring at the study site and dates limit diurnal foraging by *M.stellatarum*. The range of T_a and IR for *M.stellatarum* sites encompassed the entire range of values found at the study site and dates (C. M. Herrera, personal observation).

Despite the broad variation in IR and T_a occurring at *M.stellatarum* foraging sites and times, T_{th} remained within relatively narrow limits. This is indicative of a considerable thermoregulatory ability in this species under summer field conditions, analogous to that reported for nocturnal hawkmoths under laboratory conditions (Heath & Adams, 1965; Heinrich, 1971a, b, 1974; Hegel & Casey, 1982). Observed variation in T_{th} was significantly related to variation in T_a, and the daily rhythm exhibited by T_{th} is the natural consequence of diel rhythmicity in T_a. The highest T_{th} values (>45°C) occurred around noon, and they fall among the highest figures ever reported for hawkmoths (Dorsett, 1962; Heath & Adams, 1965; Heinrich, 1971a; Bartholomew & Heinrich, 1973; Casey, 1976; Bartholomew & Casey, 1978). Thoracic temperatures around 45°C often represent a high-temperature ceiling for insect muscular activity (Heath & Wilkin, 1970; Heinrich, 1977; Rawlins, 1980; Heinrich & McClain, 1986). The observation that *M.stellatarum* flies voluntarily at thoracic temperatures >45°C demonstrates that this species is unusually tolerant of high T_{th}. A marked tolerance to high T_{th}, probably representing a physiological adaptation to high ambient temperatures, has been reported for bees foraging in hot environments (Chappell, 1982; Cooper *et al.*, 1985; Heinrich & Buchmann, 1986), but apparently not previously for hawkmoths.

Tolerance of *M.stellatarum* to high T_{th} certainly is one of the factors enabling this species to forage during daytime in the Mediterranean summer, but its remarkable thermoregulatory capacity at high T_a doubtless is a further contributing factor. In contrast to the linear relationship ordinarily reported by previous studies of insect thermoregulation, including hawkmoths (Digby, 1955; Heinrich, 1974), the dependence of T_{th} on T_a in *M.stellatarum* was best described by a nonlinear function, and the rate of variation of thoracic temperature with T_a (the slope of the T_{th}/T_a relationship) decreased with increasing T_a. As predicted from the fitted quadratic regression, a 5°C increase in T_a from 20°C to 25°C would result in a 2.4°C increase in T_{th}, whereas the same absolute increase from 30°C to 35°C would result in a T_{th} increase of only 0.6°C. No information is available at present on the actual mechanisms involved in thermoregulation by *M.stellatarum*. At high T_a, nocturnal hawkmoths enhance heat loss by increasing blood circulation from thorax to abdomen (Heinrich, 1970, 1971b; Hegel & Casey, 1982), and the same mechanism is also to be expected in *M.stellatarum*. On the other hand, behavioural means are probably more important than physiological ones in the thermoregulation of insects in the field (Stevenson, 1985; Srygley & Chai, 1990)

In conclusion, the unusual tolerance of high T_{th} exhibited by *M.stellatarum*, and its enhanced thermoregulatory capacity at high T_a, enable this species to withstand the severe environmental conditions faced during diurnal foraging in the Mediterranean summer, and its foraging activity pattern does not seem to be seriously affected by thermal restrictions.

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