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Behavioural thermoregulation hastens spring mating activity in *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae)

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ABSTRACT

Post-diapause, overwintered adults of the true bug *Pyrrhocoris apterus* L. (Heteroptera, Pyrrhocoridae) form conspicuous aggregations at warm spots in early spring. Using a combination of laboratory experiments and field observations, we assessed the influence of this behaviour on the seasonal timing of reproduction. In the laboratory, post-diapause pairs mated after an accumulation of 80° days (dd), and females started to lay eggs after an additional 80 dd (considering 10.3 °C as a lower temperature threshold for post-diapause development). In the field, however, females mated as early as late March (based on data from four seasons), which corresponded to the accumulation of < 15 dd (based on summing the temperatures recorded at a meteorology station). Such a 'discrepancy' between laboratory and field data is explained by thermoregulation. Aggregated adults bask in sunny spots, thereby increasing their body temperatures to ~25 °C, which is 7–16 °C above the temperature of the surrounding ground. This thermal excess speeds up their post-diapause development and enables early mating and oviposition. As a result, behavioural thermoregulation hastens the seasonal start of reproduction in *P. apterus* by > 1 month.

1. Introduction

Pyrrhocoris apterus L. is a West Palearctic species that has been intensively studied since the late 1800s (Socha, 1993). Because of its massive abundance, convenient size, fast development and easy rearing, this species became a preferred model for laboratory studies of insect biochemistry, endocrinology, ecophysiology and behaviour (Socha, 1993). In the wild, aspects of dormancy (Hodek, 1968, 1971), mating (Honěk et al., 2019), reproduction (Socha, 2010), feeding (Kristenová et al., 2011) and wing polymorphism (Honěk, 1995) have been intensively studied. Surprisingly, some important facets of life history remain poorly studied, including the factors and consequences of this species' conspicuous aggregation behaviour.

Aggregation behaviours take many forms and serve several purposes (Deegener, 1918; Allee, 1931). In Heteroptera, aggregations arise passively when individuals gather at places that provide preferred conditions (Weber et al., 2018) or actively through mutual attraction of individuals to visual and olfactory cues (Youdeowei, 1969; Melber, 1982), which are also important for *P. apterus* larvae (Bongers, 1968; Schmuck, 1987, 1995). The aggregations may have different functions, e.g., bringing together individuals for mating and progeny guarding (Hibino and Ito, 1983; Carroll and Loye, 1990; Hosokawa and Suzuki, 2000; Krupke et al., 2011) or potentiating individual aposematic appearance (Aldrich and Blum, 1978).

In Central Europe, *P. apterus* has one complete generation per year, which is replenished at some sites and in some years by a partial second generation (Socha, 2010). Development takes place in the late spring and summer. Adult diapause is induced by photoperiod and completed in late December (Hodek, 1978, 1983). After the winter solstice, bugs in the wild spend the period of post-diapause development in an inactive state maintained by low temperatures (Hodek, 1968, 1988). At the start of reproduction in early spring, on sunny and warm days, the adults make large aggregations at sites where the ground surface is exposed to direct sunshine. A natural outcome of such assemblies of males and females is intensive copulation activity.

Mating in *P. apterus* has been intensively studied under laboratory conditions. Copulation is initiated during daylight hours. Males approach females, and both take a position side-by-side. The male then attaches his copulation organ to the female's genitalia, and when coupling is complete, the pair assumes the opposed position with their genitalia associated for the remainder of copulation (Žďárek, 1970). The insemination of females occurs within a few minutes after the start of the copulation, but males perform "postcopulatory mate guarding", i.e., maintain a tandem for a prolonged time, and thus prevent the females from mating with other partners (Schöfl and Taborsky, 2002). The duration of tandems varies with the body sizes of the partners.

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Tandems of small males and small females persist for the shortest times, while tandems of large females and small males persist for the longest times (Honěk, 2003).

In addition to mating, which is the main outcome of spring assembly behaviour, aggregations at warm places also contribute to body warming. We studied the thermoregulatory aspects of spring aggregation behaviour and its effect on the initiation of reproduction. This study combines five-year field and laboratory observations and addresses three topics: (i) the thermal conditions necessary for the start of post-hibernation mating activity, (ii) the timing of the start in the wild and (iii) the factors involved in active behavioural thermoregulation in the early spring.

2. Materials and methods

2.1. Sampling and rearing

In the wild, the bugs were collected at the base of lime trees (*Tilia cordata* Miller) at Krchleby (50.238N 15.024E), Prague-Hloubětín (50.104N 14.534E), Hostivice (50.081N 14.263E) and Prague-Ruzyně (50.087N 14.307E). Meteorology data (mean daily air temperatures at 2 m above the ground surface) were obtained from the meteorology station of the Crop Research Institute at Prague-Ruzyně (50.0853N, 14.2986E, altitude 338 m a.s.l.), which is situated c. 600 m from the site of Prague-Ruzyně.

For laboratory experiments, females captured in the wild were stored at 7 °C in 1 L plastic bottles, which were filled with wrapped paper and sealed with nylon fabric until use. In the experiments, bugs were held in cylindrical glass vials (10 cm diameter, 7.5 cm deep), which were sealed with nylon fabric. The bugs were fed with surplus linden (*T. cordata*) seeds spread on the bottom of the rearing vial and provided with drinking water on a moist piece of cotton. Laboratory cultures were held under a long-day (16 h light/8 h dark) photoperiod.

2.2. Determining thermal requirements for post-diapause development

Temperature is a factor that influences the rate of change of life processes. Exotherm species are adapted to particular temperature ranges. Within those ranges, as the environmental temperature decreases, their rates of development slow and finally development will cease at their lower development threshold (LDT). As temperature increases, their rates of development increase up to a temperature optimum, above which they decrease again. When data on durations of development at temperatures between the LDT and the temperature optimum are converted to their reciprocals (rates of development), the relationship between rate and temperature is close to linear. From this relationship, two constants can be calculated: (i) the above-mentioned lower development threshold (LDT) and (ii) the sum of effective temperatures (SET), a quantity equal to the number of degree-days (dd) needed to complete the developmental process of a particular development stage at any temperature within the range from the LDT to the temperature optimum (Trudgill et al., 2005).

Thermal requirements (SET) were calculated for three periods of post-diapause development: (i) a period of the whole post-diapause development from its start until oviposition (SETt), (ii) a period from the start of post-diapause development until the fertilization of 50% of females (SETa), and (iii) a period from the fertilization of 50% of females to oviposition (SETp). For these quantities, it holds that SETa + SETp = SETt. These particular SET quantities were determined in three steps using different methods.

First, thermal requirements were determined for the whole period of post-diapause development from its start until oviposition (SETt), and LDT was calculated. Experimental adults were collected at Prague-Hloubětín on 6 February 2001, when diapause was terminated (Hodek, 1978), but post-diapause development had not started because of low temperatures (the mean maximum daily temperature since the winter solstice was $+2.0 \pm 0.65$ °C and never exceeded 10 °C). On 7 February, heterosexual pairs were placed into rearing vials and held at constant temperatures of 15, 19, 21, 25 and 28 °C until the first oviposition, and each temperature treatment started with a set of 25 pairs. The mean time (days ± SE) to the first oviposition of the sets placed at each temperature was established and converted to its reciprocal, the development rate. The thermal requirements for post-diapause development (pre-oviposition period), were then calculated using the linear relationship $y = a + bx$, where y is the development rate and x is the temperature (°C). The lower development threshold (LDT, the temperature when the development rate was zero) and the sum of the effective temperatures (SETt, the number of degree days, dd units, necessary to complete development in the post-diapause period) were calculated as LDT = $-a/b$ and SETt = $1/b$.

Second, the thermal requirements for the period from fertilization of 50% of females to oviposition (sum of the effective temperatures SETp) were determined using data from experiments that investigated the timing of fertilization in the spring (see 3.2., Fig. 2). The duration of the period elapsed from fertilization to oviposition was established in a group of females sampled on 27 March 2003 at Hostivice, i.e., in the sample collected when 50% of females were fertilized. The females (N = 30) were immediately placed in laboratory conditions at 25 °C with one individual per rearing vial. The mean number of days to the first oviposition (t) was established. The sum of effective temperatures required in the period from fertilization of 50% of females to oviposition (SETp) was calculated as SETp = t*(25 [°C rearing temperature]-10.3 [°C LDT]), where t is the average time elapsed from 50% fertilization until oviposition.

Third, the thermal requirements for the period from the start of post-diapause development until the fertilization of 50% of females (SETa) were calculated as SETa = SETt – SETp.

2.3. Copulation activity and fertilization in the spring

The temporal course of fertilization in *P. apterus* populations was studied in the field over four years. The females were sampled at weekly intervals from populations in Krchleby (in 2000), Prague-Hloubětín (2002), Hostivice (2003) and Prague-Ruzyně (2004). During each year, the sampling was initiated before the start of copulation activity and finished after the whole female population was fertilized. At each sampling date, the females (N = 20 in 2000, N = 30 in 2002–2004) were immediately placed under laboratory conditions (25 °C) and held, one per rearing vial, until oviposition. The percentage of females that laid fertilized eggs was calculated using the N of females that survived until the end of the experiment. The date when 50% of females were fertilized was established using linear interpolation between the two nearest sampling dates.

2.4. Measuring ambient temperature at the site of *P. apterus* aggregation

The temperature of a site occupied by the *P. apterus* population was measured in Prague-Ruzyně on eight sunny days between 21 March and 1 April 2005, which was the period when copulation activity started. Each day, the temperature was measured in 3–4 sessions that occurred between 09:30–17:00 Central European Time (CET), which was the period when adults aggregated for thermoregulative basking. During each session, the temperature was measured at three sites, each of which was c. 5 × 5 m, which are schematically pictured in Fig. 1. They were (a) a bare site where *P. apterus* adults aggregated for basking and mating (hereafter referred to as a “lek”), (b) an insolated grassland surrounding the lek that was not occupied by aggregated *P. apterus* and (c) a site that was shaded by tree crowns. Sites (b) and (c) were within 10 m of the lek site, i.e., within a distance that we have observed *P. apterus* are able to travel. During each session at sites (a), (b) and (c), the temperature was measured at 20 randomly placed circular spots of 4 cm diameter (12.6 cm^2 area) using an optical high-performance

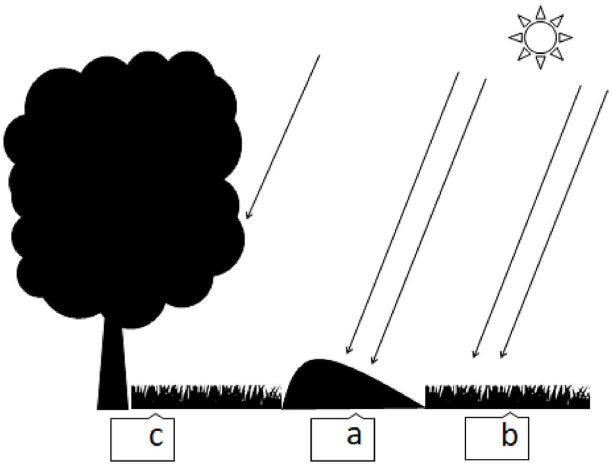

Fig. 1. Schematic representation of the site of *P. apterus* aggregation in Prague-Ruzyně, showing (a) a bare site where *P. apterus* adults aggregated for basking and mating (lek), (b) an insolated grassland surrounding the lek that was not occupied by aggregated *P. apterus* and (c) a site shaded by tree crowns.

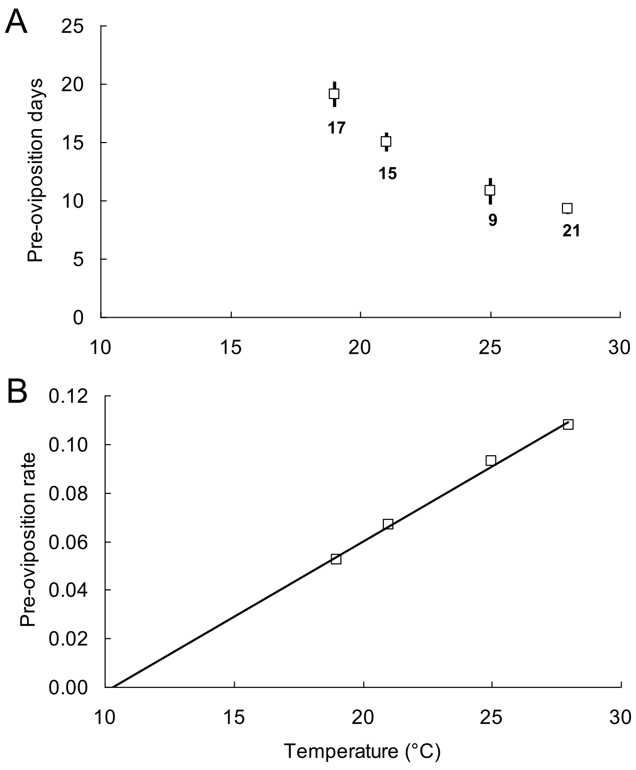

Fig. 2. The effects of constant temperatures on the post-diapause development of females (time necessary from the completion of diapause to the first oviposition). Data from a natural population from Prague-Hloubětín that was sampled on 6 February 2001 (before females started post-diapause development) and reared under laboratory conditions at 25 °C with a long-day photoperiod (16 h light/8 h dark) until oviposition. (A) The length of time (days ± SE) from collection to first oviposition at four constant temperatures, showing the duration of post-diapause development. (B) The same data converted to development rates (the reciprocals of the development durations) and fitted by linear regression [development rate] = a + b[temperature].

distance thermometer (Rayngner MX4, Fluke Process Instruments, https://flukeprocessinstruments.com). At site (a), each measured spot contained ≥ 1 *P. apterus* individual. We estimated the body temperature of the bugs at site (a) from the soil surface temperature, which is close to the temperature of a small solid object lying on it (Parry, 1951; Digby, 1955), since direct measurements of body temperature were not possible with our equipment. The average of the 20 spot measurements was calculated and considered the average temperature of the site. For each session, we calculated (i) the thermal excess of the lek spot over the insolated spot and (ii) the thermal excess of the lek spot over the shaded spot.

3. Results

3.1. Thermal requirements of post-diapause development

The thermal requirements for the entire period of post-diapause development (SETt) were calculated. Under the five constant temperatures tested, the time to first oviposition varied among post-diapause females (Fig. 2A). No females survived to oviposition at 15 °C; they either died or were discarded by day 40 of the experiment. At higher temperatures, the time to first oviposition decreased from 19.1 ± 1.09 days at 19 °C to 9.3 ± 0.43 days at 28 °C. We calculated a linear regression of development rate on temperature: [development rate] = 0.064 + 0.0062 [temperature] ($R^2 = 0.9952$, $P < 0.001$). The thermal requirements for post-diapause development were calculated as SETt = 161.3 dd above LDT = 10.3 °C (Fig. 2B).

The thermal requirements for the period from fertilization of 50% of females to oviposition (SETp) were calculated using the mean pre-oviposition period established in females that were sampled on 27 March 2003 at Hostivice and kept at 25 °C, which was 5.4 ± 0.37 days. Assuming LDT = 10.3 °C, the necessary temperature accumulation from fertilization to oviposition was SETp = 79.4 ± 1.65 dd.

The thermal requirements for the period from the end of dormancy until fertilization (SETa) was calculated as SETt-SETp = 161.3dd – 79.4dd = 81.9dd. For the rest of our study, we used approximate values of SETa = ~80 dd, SETp = ~80 dd and SETt = ~160 dd.

3.2. Copulation activity and fertilization in the spring

Copulation activity started in mid-March, with the onset of favourable weather. Each year, the proportion of fertilized females in the population (Fig. 3) increased monotonically (except in 2004, when copulation activity was suspended by a period of bad weather), and most females were fertilized within 2 weeks from the start of mating activity. In particular years, the date when 50% of females were fertilized (1 April 2000, 21 March 2002, 26 March 2003, 29 March 2004) varied by 11 days (Fig. 3).

The process of fertilization of 50% of the female population requires

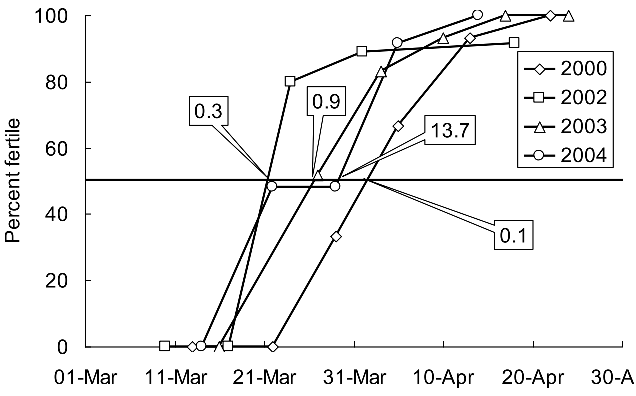

Fig. 3. The change in the percentage of fertilized females in the local populations of Krchleby (2000), Prague-Hloubětín (2002), Hostivice (2003) and Prague-Ruzyně (2004). The figures in bubbles indicate thermal sums (based on air temperatures) accumulated from the winter solstice until 50% of the females were activated (horizontal line).

the accumulation of SETa = ~80 dd. At the times when 50% fertilization was attained in the wild (Fig. 3), there were wide margins between the accumulated thermal sums and the predicted SETa. The sums of the temperatures measured using the standard meteorology data (see 2.1.) that had accumulated up to the dates of 50% fertilization were only 0.1 dd on 1 April 2000, 0.3 dd on 23 March 2002, 0.9 dd on 26 March 2003 and 13.7 dd on 29 March 2004.

In the 20-year period 1999–2018, the temperature sum necessary for the mating and fertilization of females (SETa = ~80 dd) accumulated as late as 22 April (2015) and 22 May (2010). The average date of SETa accumulation was 9 May (± 1.9 d), i.e., approximately two months later than when fertilization in the wild truly occurred (Fig. 3). The temperature sum of ~160 dd necessary for oviposition was accumulated between 8 May (2018) and 8 June (2004), with an average date of 27 May (± 1.9 d).

3.3. Ambient temperature and behavioural thermoregulation

Under natural conditions, fertilization that occurred earlier than predicted by meteorology data (3.2.) could not be completed if it was not supported by the aggregation in insolated places (leks) where warming and copulation could take place. The temperature of the lek site (site a in Fig. 1) was substantially higher compared to the surrounding insolated (site b in Fig. 1) and shaded (site c in Fig. 1) places. At Prague-Ruzyně in March 2005, the average temperature of the lek site (Fig. 4A) increased from 21.1 °C at 09:00, when thermoregulation started, to 26.2 °C at 14:00, when it peaked. The temperature at the lek site during the warm period of the day (between 11:00–16:00) was 25.3 ± 0.65 °C (mean of N = 13 observation sessions). The mean thermal excess (Fig. 4B) of the lek temperature above that of the nearby insolated grassland was 6.5 ± 0.82 °C (in particular sessions, 1.5–14.1 °C). The mean thermal excess above the shaded site, which was 16.4 ± 0.95 °C (range 8.7–22.4 °C), was greater than in the insolated grassland. The magnitude of thermal excess varied with the time of day (Fig. 4B); it was smaller near midday and increased in the morning and the afternoon.

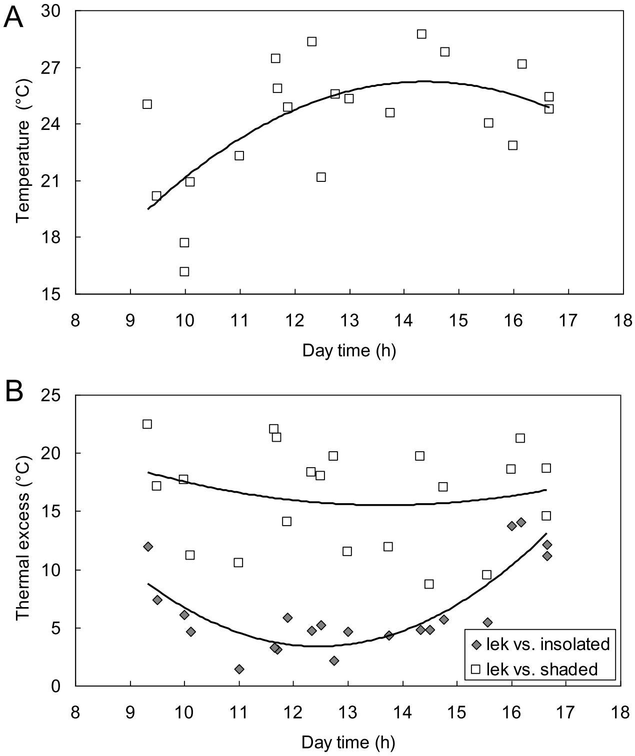

Fig. 4. The temperatures at the site of *P. apterus* aggregation in Prague-Ruzyně, measured between 21 March and 1 April 2005 and projected over a common abscissa showing the times of day when temperature observations were made. (A) Temperature at the "lek" site where *P. apterus* adults aggregated. (B) The thermal excess at the "lek" site over the temperature near the insolated place (diamonds) and near the shaded place (rectangles).

4. Discussion

This work showed the consequences of early spring aggregation behaviour of *P. apterus* in insolated places. The results concern the effects of this behaviour on the thermoregulation of adults that participate in these assemblages and the consequences of this behaviour for the life cycle of this species. Early in the spring, overwintered *P. apterus* adults aggregate in warm, insolated places. We demonstrated that this behaviour not only facilitates mating but also hastens reproduction. As a consequence of increasing body temperatures, fertilization of females starts in March, while the sums of ambient temperatures necessary for insemination are accumulated as late as May. This work both corroborated earlier data and provided new results.

First, we corroborated earlier data concerning the thermal requirements of this species. The thermal constant LDT for *P. apterus* development that we found in this study is consistent with earlier results. Our calculated LDT = 10.3 °C is close to the LDT = 12.2 °C calculated for egg development (Honěk and Kocourek, 1990) and the LDT = 12.0 ± 1.13 °C (range 9.5–14.8 °C) ascertained for larval development in different geographic populations (Lopatina et al., 2007; Balashov and Kipyatkov, 2008).

Second, in this study, we collected new data concerning the behavioural thermoregulation of *P. apterus*. The process of post-diapause development until the fertilization of 50% of females required the accumulation of SETa = ~80 dd and further development until the first oviposition required the accumulation of SETp = ~80 dd. Therefore, total post-diapause development requires SETt = ~160 dd. There was a wide margin between the thermal sum SETa and the temperatures that had accumulated in nature when 50% of the females were fertilized. Active thermoregulation behaviour, basking in insolated lek sites, effectively raised body temperatures and enabled the accumulation of the thermal sum SETa = ~80 dd that was necessary to complete fertilization of 50% of females in late March.

As in other insect species, behavioural thermoregulation is an efficient means of adapting the development cycle to the local thermal conditions (Barton et al., 2019). Passive thermoregulation, both increasing and decreasing body temperature against the ambient temperature, is an important factor that influences different processes of insect life, such as development, flight ability, finding mates, laying eggs, parental care, feeding and avoiding natural enemies and diseases (Heinrich, 1993). In *P. apterus,* behavioural thermoregulation supports the adaptation of the life cycle to the local conditions. Temperatures of ~25 °C recorded at the lek sites in the early spring were close to the 24 °C temperature preferred by larval populations in the late spring (Honěk and Šrámková, 1976). Basking in early spring hastens development in the cool period of the year. Sheltering in ground cracks during the warm period of the year (Honěk and Šrámková, 1976) slows down development and minimizes the risk of second-generation individuals dying in the autumn. The preferred temperatures of *P. apterus* were several degrees below the optimum temperature, which was likely 20 °C above LDT (Dixon et al., 2009), i.e., 30–32 °C. This difference between optimum and preferred temperatures in *P. apterus* parallels the preferences of many other exotherm species, which were summarized by Martin and Huey (2008).

The relative importance of the principal goals of *P. apterus* spring aggregation behaviour (mating or thermoregulation) as well as the behavioural mechanisms leading to the assembly of overwintered *P. apterus* individuals (mutual attraction, thigmotaxis, thermal, moisture or light preferences) remain to be studied. Nonetheless, basking in insolated places leads to increases in body temperature in the early spring, and rising body temperature is an integral part of the *P. apterus* seasonal cycle under the climatic conditions of Central Europe, which is the main message of this report.

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