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BUMBLEBEE BROOD TEMPERATURE AND COLONY DEVELOPMENT: A FIELD STUDY

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Abstract - Careful control of the brood temperature is important in view of successful colony development in social insects. Fifteen bumblebee colonies of five common Central European species in total (*Bombus hypnorum*, *B. pratorum*, *B. lapidarius*, *B. pascuorum*, *B. humilis*) were monitored for several months and the brood temperature was recorded in regular intervals to investigate the temperature range in which the colony successfully develops to produce a new generation of queens and males. Colony size was being kept track of and parasites were always promptly removed if discovered. Ultimately, all colonies in the study were successful. We observed that the colonies were very efficient with thermoregulation during the equilibrium period of the colony, with the brood temperatures between 31 and 35°C. This study presents a foundation for more detailed studies of temperature in bumblebee nests of the above species in the future.

Key words: bumblebees, thermoregulation, nest climate

Izvleček - TEMPERATURA ČMRLJEGA SATJA Z ZALEGO IN RAZVOJ GNEZDA: TERENSKA RAZISKAVA

Eden od pomembnih dejavnikov, ki vplivajo na uspešen razvoj družine čmrljev, je skrbna regulacija temperature zalege. V naši študiji smo več mesecev opazovali petnajst družin čmrljev petih pogostih vrst srednje Evrope (*Bombus hypnorum*, *B. pratorum*, *B. lapidarius*, *B. pascuorum*, *B. humilis*). Spremljali smo temperaturo zalege, da bi ugotovili, v kakšnem temperaturnem območju se družina uspešno razvije do izleta novih matic in samčkov. Poleg tega smo spremljali velikost posameznih družin in odstranili parazite, če so se pojavili. Vseh petnajst opazovanih družin je bilo uspešnih. Ugotovili smo, da je termoregulacija učinkovitejša pri družinah in vrstah, ki imajo več delavk. V ravnovesnem obdobju je bila temperatura zalege med 31 in 35°C. Študija predstavlja temelje za podrobnejše študije pogojev v gnezdih čmrljev v prihodnosti.

Ključne besede: čmrlji, termoregulacija, temperatura v gnezdu

Introduction

Bumblebees (genus *Bombus* from the bee family Apidae) are important pollinators of various plants. Similar to domestic honeybees, they are social insects that live in colonies. However, they are bulkier in constitution and able to generate considerable quantities of metabolic heat, using it to maintain stable body temperatures many degrees above the ambient temperature (Goulson, 2003). This allows them to forage at lower temperatures and even in rain. In addition, bumblebees employ a technique called buzz-pollination or sonication (De Luca and Vallejo-Marin, 2013) to extract pollen from flowers of certain plants which release pollen through small openings in the anthers' tips by shaking the anthers – a technique that the honeybees are not capable of. This way, bumblebees are the key pollinators of plants such as clover or tomatoes. Bumblebee flight buzzing sounds of some common Central European bumblebee species were the focus of our previous research (Gradišek et al., 2017).

In the wild, different bumblebee species build their nests in different natural environments according to the opportunities and characteristics of the surrounding. Many species build their nests in the abandoned burrows of small rodents in the ground while other build their nests on the surface of the ground within tussocks of grass and brushwood, and even in abandoned birds' nests, squirrels' drays, and artificial cavities (Goulson, 2003). Their goal is to find a place that provides enough space for brood development and shelter from rain, predators, and temperature extremes. Insulation allows the bumblebees to conserve the metabolic energy required for thermoregulation. According to practitioner experiences (Grad et al., 2010; Grad et al., 2016), in the anthropogenic environment, the bumblebees exploit man-made objects as possible nesting sites.

In the nest, one of the most important tasks of the colony is to keep the nest temperature as constant as possible to allow successful development of the brood placed inside the comb. A queen starts building the nest in late winter or early spring, when the air temperatures can still vary for a short time from rather low temperatures approaching 0°C up to comfortable ones of about 15°C. The timing depends very much on queens' species, their natural requirements where to place the nest, and their abilities to maintain the necessary nest temperature (Goulson, 2003; Heinrich, 1979). During the cold periods, the queen (and later also the workers) provide heat to the brood by thermogenic activity of thoracic muscles (Masson et al., 2017). By modulating their metabolic activity, the adults are able to regulate their abdominal temperature and therefore maintain the brood temperature within a narrow range (Jones and Oldroyd, 2007). On the other hand, in late spring and summer, the outside temperatures rise and the nest has to be cooled down to prevent it from overheating – the larvae can develop malformations or die if the temperatures surpass a certain threshold. Overheating is prevented by fanning, which becomes the task of the workers that have emerged from the nest by now. The nest temperature was studied by several authors. Seeley and Heinrich (1981) note that the optimal temperature in a nest with a large number of workers is around 30-31°C. Heinrich (1994) studied *B. vosnesenskii* and *B. polaris* and found out that the brood temperature can vary from 24 to 34°C. Weidenmüller (2004) studied fanning behaviour in *B. terrestris* as being triggered by increased temperature and CO_2 concentration in the nest. In the experiment, the heating of the nest went up to about 30°C. This study marks the temperature around 27.7-28.7°C as favourable while higher temperatures resulted in increased fanning intensity. Weidenmüller et al. (2002) also found that larger bumblebee colonies (of 60 or more individuals) responded to environmental perturbations faster and more efficiently than the smaller ones. Other authors (Hagen, 1994, Hintermeier, 1997, Matheson, 1996, Witte and Seger, 1999) state that the temperature in the nest is 30-32°C while the temperature of the comb that contains no brood can be a couple of degrees lower. According to Heinrich (2001) temperatures below 30°C are generally considered to inhibit the growth and may cause developmental damage in bumblebee species. Dean (2016) studied thermal stress in *B. impatients* by exposing late-stage larvae to sub-lethal heat and cold stress (16-35°C). The stress resulted in some workers developing abnormal colour patterns, although no statistically consistent colour change response was observed. Schultze-Motel (1991) studied temperature fluctuations in a *B. lapidarius* nest, placed in a calorimeter box connected to the outside to allow normal foraging outings. The brood cell temperatures were maintained between 27 and 32°C while the fluctuations of the heat loss were measured as well, they typically showed a sinusoidal fluctuations through the day. In 1950s, Fye and Medler (1954) performed a field study of three North American species (*B. borealis, B. rufocinctus*, and *B. fervidus*) using thermocouples installed in the nests to check the daily temperature fluctuations. They found that the brood temperature was about 30°C, with the temperature fluctuating more when a smaller number of workers was present.

In studies of similar social insects, Cook et al. (2016) studied fanning behaviour in honeybees (*Apis mellifera*) in response to different rates of increasing temperature; the authors state that the bees keep the temperature of the nest below 36°C. On the other hand, Höcherl et al. (2016) studied nest thermoregulation in paper wasp *Polistes dominula* that build combs without the cover and are therefore more sensitive to thermal fluctuations. They found out that instead of fanning, the main mean of cooling is the evaporation of water that the wasps bring to the nest.

In the studies mentioned above, the systematic studies of temperature variations in a nest and the bumblebee response were typically conducted in laboratory settings and over short timeframes, except for the study of Fye and Medler (1954) that took place in the field. In our observation-based field study, we were interested in the temperature in bumblebee nests developing in suitable nest-boxes (bumblebee hives) in the field over a longer time period, covering most of the lifetime of the colony, in response to the developmental stage of the colony, outside temperatures, and other external influences, such as the infestation with parasites. We focused on the temperature of the brood cells, as the proper temperature interval of the brood allows for successful development of a new generation. Fifteen colonies of five bumblebee species in total were monitored, starting roughly with the emergence of the first workers and concluding after the first young queens and males of the new generation started to emerge from the nest, thus ensuring the survival of the species in the following year. We were monitoring the temperature of the brood, the external temperature, and the number of individuals in the nest. In accordance with the literature (Schultze-Motel, 1991), the consecutive stages of the colony development are as follows: (1) *The period of upbringing* is the time interval after the old queen has started to collect pollen for the first batch of the brood until the workers of the batch have started to forage. (2) *The equilibrium period* sees a large number of workers and ends when young queens and males start to fly out of the nest to mate. (3) *The period of decline* follows the equilibrium and ends when there is no more brood in the comb cells of the nest. Ultimately, all bumblebees, except the young queens, perish.

To our best knowledge, this is the first multi-species temperature study of some common bumblebee species of Central Europe spanning over several months. The main aim of the presented study was to look at temperature intervals which allow the bumblebee colonies to develop to the stage where they produce new queens and males, thus ensuring the survival of the new generation. Our study further presents a useful ground for more detailed studies in future, with aims in finding optimal rearing temperatures for research on bumblebees, to understand thermal requirements across species, and to understand what factors contribute to ability to control the thermal environment of the nest.

Materials and methods

Fifteen bumblebee colonies of five different bumblebee species (*B. hypnorum*, *B. pratorum*, *B. lapidarius*, *B. pascuorum*, *B. humilis*) were monitored in the study, as listed in Table 1. The colonies have been brought up by the queens that had hatched at the place the previous year and had returned back to their hatching place in spring – this determined the species and the number of colonies per individual species included in the study. The nest-boxes were made of wood, of standard design used for this purpose (see for example Prys-Jones and Corbet, 1987). Single-chambered boxes are more suitable for species that build nests on the surface of the ground (such as *B. humilis, B. pascuorum, B. ruderarius*) while double-chambered boxes (containing an ante-chamber) are more likely to be populated by the species that build nests under the surface, such as *B. lucorum, B. terrestris, B. hortorum, B. argillaceus, B. sylvarum, B. pratorum, B. haematurus, B. hypnorum*, but can also be populated by the surface species (author's observation).

The nest-boxes were located in the village of Petelinje, Dol pri Ljubljani municipality, Slovenia (elevation 270 m, moderate continental climate (Köppen climate classification: Cfb)). The nest-boxes were protected from direct sunlight during most of day, receiving it only up to 9 am the latest. The study took place during the spring and summer months of 2017. The spring of 2017 in Slovenia was marked by a warm period in March, followed by an unusually cold spell in April, causing the collapse of several bumblebee colonies where the brood was already developing. The colonies in our study survived the cold.

Table 1: Bumblebee colonies monitored in the study, denoting the dates of important events for the colony (all in 2017), together with the average equilibrium brood temperature.

Colony designation	Queen enters the nest-box	Measurements begin	First new queen leaves	Parasites removed	Measurements end	Average equilibrium brood temperature
B. pratorum	23.3.	17.5.	21.5.	/	7.6.	31.9 °C
B. hypnorum 1	21.3.	18.5.	2.6.	22.7.	10.6.	34.5 °C
B. hypnorum 2	24.3.	18.5.	1.6.	24.7.	10.6.	33.2 °C
B. hypnorum 3	29.3.	18.5.	30.5.	27.7.	10.6.	34.2 °C
B. hypnorum 4	30.3.	18.5.	30.5.	/	10.6.	32.5 °C
B. lapidarius 1	23.3.	19.5.	21.7.	24.6.	25.7.	32.9 °C
B. lapidarius 2	10.4.	18.5.	20.7.	4.8.	25.7.	32.6 °C
B. pascuorum	7.4.	20.5.	16.8.	25.8.	25.7.	32.5 °C
B. humilis 1	3.4.	22.5.	22.7.	/	26.7.	33.9 °C
B. humilis 2	9.4.	22.5.	21.7.	/	26.7.	33 °C
B. humilis 3	10.4.	23.5.	16.7.	26.7.	26.7.	33.8 °C
B. humilis 4	14.4.	21.5.	9.7.	/	25.7.	33.1 °C
B. humilis 5	2.5.	23.5.	18.7.	/	26.7.	33.1 °C
B. humilis 6	1.5.	22.5.	18.7.	/	26.7.	33.7 °C
B. humilis 7 *	13.6.	24.6.	22.8.	/	25.7.	31.4 °C

* This colony was moved from a meadow ground into the nest-box on 13 June, already containing a queen and two workers. The average temperature for this colony spans over the whole observation period.

The brood temperature was measured using a conventional digital probe thermometer (TFA LT-101, Conrad Electronic SE). For each of the measurements, the nest-box was opened and the tip of the probe was placed on the surface of the comb containing brood and the maximum temperature was recorded by probing several parts of the comb (it should be stressed that some parts of the comb, especially toward the edges, had temperature up to 3°C lower). For *B. hypnorum* families, with large numbers of aggressive workers, the operator had to wear a full beekeeping gear for protection, while the measurements were always carried out around noon or in early afternoon *in situ*, in order not to further provoke the workers. For other four species, the measurements were carried out in the evening or early in the night, either *in situ* or with the nest-box being carried indoors for the measurement for convenience reasons (better light conditions). Here, we always assumed that the heat capacity of the comb is sufficiently high that the temperature does not change significantly during the time required to (quickly) remove the nest insulation, push the probe inside the nest, cover the nest, and perform the measurements. In our study, the use of a probe thermometer was seen as more appropriate than the use of thermocouples – as the latter would represent a permanent foreign object in the nest while the thermometer only causes a temporal disturbance. In addition, a probe thermometer allows us to determine the parts containing the brood more precisely.

The beginning of the temperature measurements roughly coincided with the emergence of the first workers. For each of the measurements that were first carried out on weekly basis and later in 10-day intervals, the following data were recorded: brood temperature, time of the measurement, external air temperature together with daily maximum and minimum, and the number of workers in the nest. For most colonies, the measurements concluded some days after the first new queen left the nest. An exception was the *B. pascuorum* nest due to its rather long life cycle, where the measurements ended some days earlier. Following the conclusion of the temperature measurements, the nests kept being monitored for general health of the bumblebee colonies. During the course of the development, some colonies were infested by a wax moth (*Aphomia sociella*), a common bumblebee parasite. In most cases, this took place after the temperature measurements had already concluded. The parasites were removed from the nest immediately after being observed for the first time, and it appears that all colonies continued with the development normally afterwards.

At each measurement, we estimated the family size. As the measurements mostly took place in the evenings when the bees were in the nest-boxes, it was straightforward to count/estimate both the number of workers and new queens in the open box.

Results

All monitored bumblebee colonies underwent a successful development cycle – from the old queen building a nest and laying eggs, through the hatching of the first workers, to the hatching of new queens and males that left the nest. The development of the colony differs from species to species. While the *B. pratorum* colony produced first new queens already in May and declined in mid-June, other species, such as *B. humilis* and *B. pascuorum*, only started producing first workers in late May but continued to thrive well into August. In the colonies with large numbers of workers, fanning behaviour was observed when the outside temperatures exceeded 32°C in shade.

The general observation is that the temperature of the brood for all colonies was roughly between 30 and 35°C throughout the equilibrium period of the colony while the temperature was somewhat lower during the upbringing period with a small number of workers (as seen in most colonies) and during the decline (as seen in *B. pratorum*). For all colonies except for *B. pratorum*, we noticed the transition between the upbringing and the equilibrium periods when the number of workers increased significantly. When the measurements started, the *B. pratorum* colony already was in the equilibrium period and entered the decline in the last week. Other colonies were still in the equilibrium when the measurements concluded with the new queens hatching.

Figs. 1 and 2 show the measured brood temperature together with the colony size. Fig. 1 shows the data for eight colonies of four species while Fig. 2 shows the data for seven *B. humilis* colonies. Fig. 3 shows detailed measurements of selected colonies, one representative example per each species. In the following, we first look at each species individually and then at some general observations.

In the single colony of *B. pratorum* monitored, the queen moved to the nest-box in late March. The first new queens appeared in the second half of May and the colony already lost the old queen in early June. The maximum number of workers

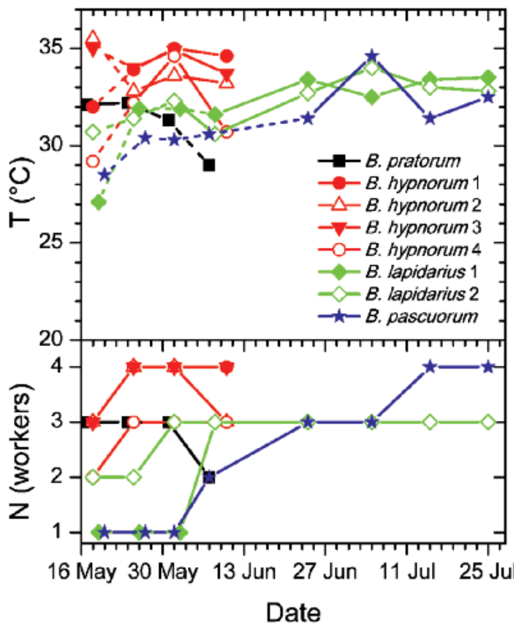

Figure 1: Top: brood temperature in the nests of *B. pratorum, B. hypnorum, B. lapidarius,* and *B. pascuorum*. *Dashed line* indicates the upbringing period while the *solid line* indicates the equilibrium period, reflecting the increase in the worker numbers. Bottom: number of workers in a colony at a given date. The legend for the number of workers on y-axis is the following: 1 is less than 10, 2 is between 10 and 20, 3 is between 20 and 100, and 4 is above 100 workers.

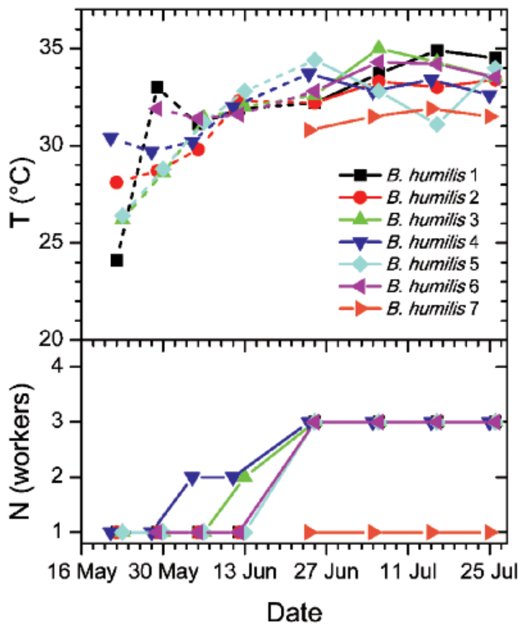

Figure 2: Top: brood temperature in the nests of seven colonies of *B. humilis*. *Dashed line* indicates the upbringing period while the *solid line* indicates the equilibrium period, reflecting the increase in the worker numbers (note that *B. humilis* 7 never exceeded 10 workers). Bottom: number of workers in a colony at a given date, the legend on the y-axis is described in Fig. 1.

recorded in the nest was about 100 and about 5 new queens hatched. The average brood temperature during the equilibrium period of the colony was 31.9°C while the temperature dropped to 29°C during the decline, when the comb was almost devoid of new larvae.

In *B. hypnorum* colonies, the queens moved to the nest-boxes within the last ten days of March and new queens emerged from all four nests at the end of May/beginning of June, within four days. In colonies 1-3, the colony development followed a very similar pattern: at the beginning of the temperature measurements on 18 May, there were around 20 workers in the nest already. Within the following weeks, the number of newly hatched workers increased above 150. About 15 to 20 new queens hatched in each colony. The average brood temperature during the equilibrium period was 34.5°C for colony 1, 33.2°C for colony 2, and 34.2°C for colony 3. Colony 4 was smaller in numbers in comparison to other three, starting with less than 20 workers at the beginning of the measurements (with consequently lower temperature of 29°C). In the following three weeks, the number of workers increased to about 80, about 5 new queens hatched. The average temperature during the equilibrium period was 32.5°C. In all four cases, the deviations from the average value were always below 2°C.

The two queens of *B. lapidarius* settled their nests with the time difference of 17 days, however, the first new queens emerged from both nests almost simultaneously. Colony 2, the queen of which settled in the nest later, grew the number of workers above 150 and about a week earlier than colony 1 with the maximum number of workers about 60. Colony 1 produced about 5 new queens and colony 2 about 20. During the equilibrium period, the average temperature was 32.9°C for colony 1 and 32.6°C for colony 2. Again, the deviations from the average were below 2°C. Colony 1 had nest infestation with the wax moth in the middle of the observation period, however, a quick discovery and removal of the parasites resulted in no apparent changes of the colony development. In comparison, other cases of nest infestation took place after the first new queens have already left the nests.

The queen of *B. pascuorum* entered the nest-box in early April. In the second half of May, there were still less than 10 workers in the nest, while by mid-July, there were over 100. About 10 new queens hatched in the colony. During the equilibrium period, the average brood temperature was 32.5°C.

B. humilis represented the largest set in the study, with seven colonies, one of which (colony 7) was moved from the field to the nest-box in mid-June as an already formed nest. The queens of colonies 1-6 moved to the hives sometime between the beginning of April and beginning of May. In late May and early June, these colonies contained small numbers of workers (about 10 or less), only on 25 June, the number of workers increased above 20. New queens emerged within the span of 10 days in mid-July, showing no apparent link to the time the old queens settled in the nest-box. In *B. humilis*, we could observe how the brood temperature is rising with the increasing number of workers until it becomes more or less constant when a large number of workers is present (equilibrium period). The maximum number of workers in these six colonies was somewhere between 60 and 80 while the number of new queens was between 5 and 10. In the early stages, the temperature could be as low as 24.1°C (colony 1). During the equilibrium period, the average brood temperature was 33.9°C for colony 1, 33°C for colony 2, 33.8°C for colony 3, 33.1°C for colony 4, 33.1°C for colony 5, and 33.7°C for colony 6. Colony 7 never grew above 10 workers and the first new queen (only two new queens emerged in total) only appeared in the second half of August. The average temperature during the observation period was 31.4°C. In all *B. humilis* nests, the deviations from the average temperature during the equilibrium period were even smaller than in other species, below 1.5°C.

Following the conclusion of the temperature measurements, the status of the colonies was checked occasionally. Six more colonies saw the infestation with the wax moth which was removed upon discovery. The life span of the colonies was similar to what was expected for particular species based on the previous observation. The old queens died before the last workers did, although it is difficult to pinpoint the time of death of the queen without opening the nest-box. The last workers of *B. pratorum* died on 12 July, *B. hypnorum* between 13-27 July, the two *B. lapidarius* colonies on 14 August and 8 October, respectively, while some individual workers of *B. humilis* and *B. pascuorum* survived up to the first week of November.

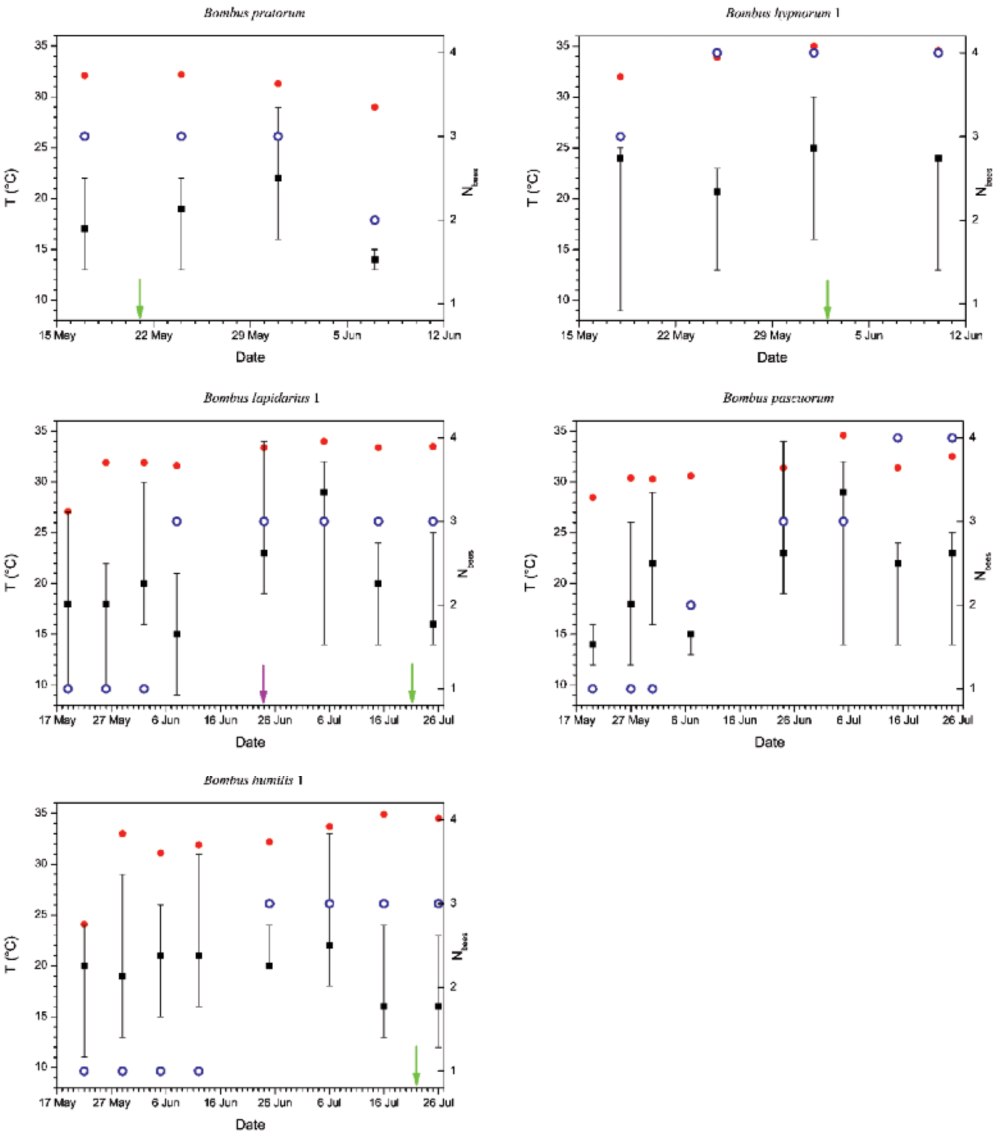

Figure 3: Colony development plots for five selected bumblebee colonies. *Red circles* represent the brood temperature. *Black squares* represent the external temperature at the time of the measurement while the error bars correspond to the maximum and minimum temperatures of the day the measurement took place. *Blue empty circles* (legend at the right side) indicate the estimate of the colony size as discussed in Fig. 1. *Green arrow* indicates the date the first new queens left the nest while the *purple arrow* in *B. lapidarius* 1 plot indicates the day the wax moth parasite was removed from the nest-box.

In all colonies, the brood temperature measurements are in a good agreement with the related work mentioned in the introduction. Throughout the equilibrium period, the brood temperature was between 31 and 35°C, the deviations from the average temperature for individual colony were less than 2°C and for *B. humilis* even below 1.5°C. Especially in *B. humilis*, the relation between the colonies size and the efficiency of thermoregulation is clearly visible, with the brood temperature being lower during the upbringing and roughly constant during the equilibrium with a large number of workers being more efficient in thermoregulation than small numbers.

Discussion

In the area around Ljubljana, based on the observations by the authors in the years 2010-17, the queens of the most common Slovenian bumblebee species (*B. lucorum, B. terrestris, B. hypnorum, B. hortorum, B. pratorum, B. haematurus, B. lapidarius, B. argillaceus, B. pascuorum, B. humilis, B. sylvarum*, and *B. ruderarius*) in general emerge from their winter hibernation sites in March and first ten days of April (Grad et al., 2010; Grad et al., 2016). Sometimes queens of *B. lucorum* or *B. terrestis* emerge already in February, queens were already observed for example on 29 February 2012 and 14 February 2014. The year 2013 was exceptional; due to a wet and snowy March the queens emerged no earlier than between 11-19 April. Later on, many of these queens would perish due to cold and wet weather intervals. As seen in Table 1, in 2017, the queens in our study entered the nest-boxes between the second half of March and early May.

The long-term studies of the temperature in the bumblebee nests of Fye and Medler (1954) and Schultze-Motel (1991) used thermocouples inserted inside the nest. When designing our experiment, we decided against this approach, as the thermocouple is a foreign object in the nest. Based on our previous experience, bumblebees tend to avoid foreign objects, which could influence the measurements. In addition, the queen after the first hatch lays eggs on top of the comb in different places, meaning that the thermocouple would no longer be at the ideal position. On the other hand, a quick measurement with a probe thermometer allows a precise measurement of the maximal brood temperature. Here, we think it is safe to assume that an occasional comb cover removal in order to place the probe thermometer on the top of the brood-containing cells and an immediate covering back the comb afterwards represents a negligible influence on the long-term dynamics of the colony and also that the heat capacity of the brood-containing comb is sufficiently high so that the temperature remains constant during the time of the measurement (that takes under five minutes). Following the analysis of the results, we decided to repeat the study in future, using thermocouples to continuously monitor the temperature in the nest-boxes. However, they should be repositioned every couple of days in order to be located close to the brood.

During the days the measurements took place, the outside temperature was almost always lower than the brood temperature. In addition, the nest-boxes were located in shade and not exposed to direct sunlight, therefore no overheating of the brood took place – also reflected in the fact that all colonies in the study were successful in raising new queens and males. In both the studies of Fye and Medler (1954) and Schultze-Motel (1991), it was observed that the fluctuations of the temperature were typically around 2°C around the average during the day. This is also in agreement with the variations in the temperature between our individual measurements. The fanning behaviour was observed in the colonies with large number of workers when the outside temperature was above 32°C in shade, which is consistent with the reports of Weidenmüller (2004). On the other hand, in future studies, we also plan to monitor the air temperature in the nest-boxes to establish the relationship between the air and brood temperature in the observed species.

Conclusion

In the 15 bumblebee colonies of 5 species studied, the brood temperatures were between 31 and 35°C during the equilibrium period, within each colony, the temperature fluctuations were up to 2°C around the average value. As all colonies survived and successfully produced new queens and males, this temperature range is favourable for brood development, which is in agreement with previous research on the topic, although on different bumblebee species. In all species studied, the colony development cycle was in line with the observations from previous years. The brood temperature was observed to be lower during the upbringing and the decline periods when there is a smaller number of workers present in the nest. During the study, the outside temperature was typically lower than the brood temperature, indicating that the workers are efficient in thermoregulation when it comes to heating the brood. As seen well especially in *B. humilis*, thermoregulation is more efficient when there is a larger number of workers in the colony, which is reasonable. As there were no prolonged periods of heat and the nest-boxes were not exposed to direct sunlight, there were no cases of the colony overheating – although fanning behaviour was observed when the outside temperature exceeded 32°C in shade.

The study was set out as a season-long field study with as little interference as possible in order to properly reflect the field conditions. In future, we plan to equip several nest-boxes with a series of thermocouples to continuously monitor the temperature fluctuations in different parts of the nest and to study how quickly different species react to changes of the conditions outside.

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