SHORT COMMUNICATION

Higher developmental temperature increases queen production and decreases worker body size in the bumblebee *Bombus terrestris*

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Abstract

Climate change and increasing average temperatures are now affecting most ecosystems. Social insects such as bumblebees are especially impacted because these changes create spatial, temporal and morphological mismatches that could impede their ability to find food resources and mate. However, few studies have assessed how the colony and life cycle are affected when temperatures rise above optimal rearing temperature. It has become imperative to understand how heat stress affects the life history traits of insect pollinators as well as how changes in life history interact with other traits like morphology. For example, a decrease in the number of foraging workers could be balanced by producing larger workers, able to forage at longer distances and gather more resources. Here, we investigated the impact of temperature on colony production and body size in the bumblebee *Bombus terrestris*. Colonies were exposed to two temperatures: 25 °C, which is around the optimal temperature for larval development and 33 °C, which is slightly above the set-point that is considered stressful for bumblebees. Although the production of males and workers wasn't significantly affected by these different temperatures, queen production and reproductive investment were much higher for colonies placed in 33 °C than in 25 °C. We also found that, in agreement with the temperature-size rule, workers were significantly smaller in the higher temperature. The decrease in worker body size could affect resource collection and pollination if their foraging distance and

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the quantity of food they are taking back to the colony decreases. While in our controlled conditions the bumblebees were fed *ad libitum*, the decrease of resource collection in field conditions could prevent colonies from producing as many queens as in our study. Together with the decrease of worker body size, our results suggest that elevated temperatures could ultimately have a negative impact on bumblebee colony fitness. Indeed, smaller workers are known to have weaker flight performance which could affect foraging performance and consequently colony development.

Introduction

Over the past few decades, climate change has led to increasingly unpredictable weather patterns (Thibeault and Seth 2014) like heat waves (Perkins-Kirkpatrick and Lewis 2020), and will raise the global average surface temperature by 0.3 °C to 4.8 °C before the end of this century (Pachauri et al. 2014). These changes have a wide range of consequences on many animal species by affecting geographical range and phenology, disrupting ecological interactions and potentially altering their ability to perform ecosystem services (Bale et al. 2002; Buckley et al. 2017). Life-history traits related to life cycle and reproduction are central for the fitness of organisms and are particularly useful in helping us to understand how species will respond to a warming world. For example, insects are known to develop faster under warmer conditions, potentially leading to an increase in the number of generations (Altermatt 2010; Hamann, et al. 2020). Amongst insects, pollinators are particularly important both for the ecosystem services they provide us, as well for the central role they play in the pollination of many wild plant species (Gallai et al. 2009; Ollerton et al. 2011). While the effects of climate change on insect pollinators are still mostly theoretical and based on model predictions in the early 21st century, recent studies have shown that it is already having a negative effect on them (Kammerer et al. 2020; Soroye et al. 2021). For instance, global warming affects plant-pollinator interactions, creating potential spatial, temporal and morphological mismatches (Hegland et al. 2009; Miller-Struttmann et al. 2015; Pyke et al. 2016; Gérard et al. 2020). While informative, these studies do not consider the potential impact of warming on life history traits, such as the number of individuals produced – particularly sexuals (*i.e.* queens and males in social bees) – or the timing of their production, which is important for understanding the impact on reproduction, pollination and life cycles. In bees, for example, warmer rearing conditions can decrease development time (Radmacher and Strohm 2010), advance emergence date (Duchenne et al. 2020) or increase mortality before emergence (O'Neill et al. 2011). Strong evidence that increased temperatures can affect the life cycle of bee colonies comes from Mediterranean populations of bumblebees (Rasmont et al. 2005, 2008; Goulson 2010). Mediterranean *Bombus terrestris* colonies aestivate during the warm summer instead of hibernating during winter (Rasmont et al. 2008) and this same species is increasingly active during the winter in UK. Moreover, while most of bumblebee species have one colony cycle *per* year (Goulson, 2010), Mediterranean populations of *B. terrestris* tend to have two colony

cycles *per* year (Rasmont et al. 2005). Further evidence that elevated temperatures affect bumblebee life cycles comes from the UK, where *B. terrestris* are becoming increasingly active during the winter (Edwards 2006; Farmer 2006; Hart et al., 2021). In addition to this field-based work, several studies have also assessed the impact of rearing temperature on colony development in controlled conditions. Favourable temperatures for colony development vary between species and studies. Indeed, different studies identified 25 °C (Holland and Bourke 2015), 27–29 °C (Weidenmüller et al. 2002) or 28–30 °C (Nasir et al. 2019) as optimal temperatures for colony longevity, individual longevity, colony productivity as well as thermoregulatory behaviour. The temperature at which bumblebees increase fanning intensity (indicating heat stress) also differs between studies – from 29 °C (Weidenmüller et al. 2002) to 32 °C (Grad and Gradisek 2018) – leading to changes in the allocation of energy towards thermoregulation, which may affect other aspects of colony life. As bumblebees are social insects, the colony itself is characterized by its own development, notably in terms of number of individuals or sexuals produced (Wilson 1985; Holland et al. 2013). However, the effect of increased developmental temperature on colony productivity and life history traits remains unclear. Here, we address this knowledge gap by experimentally investigating how elevated developmental temperatures affect the life history traits of *B. terrestris* colonies. We assess how caste production (*i.e.* queens, workers and males), as well as reproductive investment, are affected by high rearing temperature and how individual body size from these castes varies depending on the temperature. Taking body size into consideration is crucial, as lower worker production could be compensated by larger body size. Indeed, larger individuals can have higher foraging performance and larger foraging ranges, which might compensate for the potential decrease of foraging efficiency due to lower worker production (Spaethe and Weidenmüller 2002; Greenleaf et al. 2007; Klein et al. 2017). We assess the variation of these features at two temperatures: 25 °C – which is a temperature commonly experienced by bumblebees in temperate regions during spring and summer and can be an optimal temperature for colony development (Holland and Bourke 2015) – and 33 °C, which is slightly above the set-point at which bumblebees increase fanning behaviour and is considered as a stressful condition (Vogt 1986; Weidenmüller et al. 2002; Grad and Gradisek 2018). With the increase of heat wave frequency (i.e. prolonged periods of excessive heat; Perkins-Kirkpatrick and Lewis 2020), this stressful temperature is also becoming ecologically relevant during summer in many European countries. We hypothesized that colonies reared at 33 °C may have lower production due to stressful temperature and that the individuals produced will have smaller body size than bumblebees reared at 25 °C, as predicted by the temperature-size rule (TSR; Atkinson 1994; Angilletta and Dunham 2003).

Methods

Biological models

The experiments were conducted over two sessions, each lasting two months: session 1 occurred during winter 2020 and session 2 during spring 2021. In each session, eight

colonies of *Bombus terrestris audax* (Koppert, Berkel en Rodenrijs, The Netherlands) were used (making 16 colonies in total). The colonies were kept in the dark at 50% humidity, in temperature-controlled incubators (Panasonic MIR, 123L) at the Department of Zoology in Stockholm (Sweden) – four colonies were incubated at 25 °C and four at 33 °C. The experimental colonies were placed in wooden nest boxes (28 cm × 16 cm × 11 cm). Pollen was delivered every two to three days (Naturprodukter, Rawpowder Bipollen) inside the colony. *Ad libitum* 30% sucrose solution (w/w) was available all times *via* a gravity feeder. After 25 days of development, all individuals in each colony were marked. Thus, at day 26, each newly emerged individual had experienced the temperature treatment throughout the entirety of its development, as 25 days corresponds to the duration of worker development (Duchateau and Velthuis 1988). All males and queens included in the analysis emerged after day 26, so that they also experienced the full temperature treatment during their development. One of the colonies reared at 25 °C during session 1 was removed from the analysis because the queen died at the beginning of the experiment, thus inducing a bias in the number of individuals produced by this colony. In total, we gathered a dataset of 2834 workers (n = 1460 at 25 °C from seven colonies, n = 1374 at 33 °C from eight colonies), 182 males (n = 65 at 25 °C from seven colonies, n = 117 at 33 °C from eight colonies) and 182 queens (n = 2 at 25 °C from seven colonies, n = 180 at 33 °C from eight colonies).

Body size measurements

The inter-tegular distance (ITD, *i.e.* the minimal distance between the tegulae; the coverings over the wing bases) was used as a proxy for body size (Cane 1987) and was measured using a digital calliper (Cocraft, Insjön, Sweden).

Statistical analyses

First, we used separate Wilcoxon tests to assess if there were differences in (i) the total number of individuals, (ii) the total number of individuals in each caste separately and finally (iii) the reproductive investment between the colonies. Reproductive investment is defined as the percentage of sexuals (males and queens) on the total number of individuals produced in a colony. If the ratio is higher, it thus means that the proportion of sexuals is higher.

　　After checking assumptions, we built linear mixed models (LMM; lmer4 R package) to understand the impact of rearing temperature on body size. We computed two different models for males and workers, as their body size differs significantly. If these assumptions were not verified even when using log- or rank transformation, we built Generalized Linear Mixed Model with a Gamma distribution (GLMM). This distribution is adapted for non-normal positive and continuous data. We fitted the models with body size (ITD) as a response variable, included temperature as a fixed effect, and colony ID and session number as random effects. We selected the best model using AIC criteria (Burnham and Anderson 2004) after testing all possible combinations.

Results

Colony development

First, the session did not have any significant impact on any parameter of the colony development (all p-values > 0.05). The temperature treatment did not affect the total number of individuals (p = 0.96), males (p = 0.24) or workers (p = 0.34) produced by each colony (Fig. 1). However, the number of queens produced was significantly higher at 33 °C (p = 0.001; Fig. 1). While the first queen appeared after 28 days of development at 33 °C, the first queens from 25 °C appeared after 39 days. In both temperature treatments, the first males appeared after 26 days of development. The reproductive investment was also significantly higher for bumblebees reared at 33 °C (p = 0.02).

Body size

The model that best explained the variation in body size of males included temperature and colony ID (Marginal R-squared = 0.02; Conditional R-squared = 0.27). No significant impact of the rearing temperature was observed (p = 0.53; Fig. 2). The random factor colony ID explained 25.7% of the variance that remained in the residuals after the variance explained by the fixed factors was removed. The model that best explained the variation in body size of workers included temperature, session and colony (Marginal R-squared = 0.1; Conditional R-squared = 0.28). The body size of workers reared at 33 °C was significantly smaller than those reared at 25 °C (p = 0.006; Fig. 2). The random factors colony ID and session number explained 6.3% and 14.1% of the variance that remained in the residuals, respectively. Variance in body size in males and workers was not affected by rearing temperature (p = 0.73 and p = 0.49 respectively). Due to the low number of queens produced at 25 °C, we were not able to assess the impact of temperature on their body size.

Discussion

Here, we investigated the effect of elevated developmental temperatures on bumblebees by measuring the production and body size of colonies kept at two different developmental temperatures – one that is optimal for larval development (25 °C) and one that causes heat stress (33 °C). Overall, we found that only queen production and reproductive investment were significantly affected by the elevated temperature. We also found that workers that developed under the elevated temperature had a smaller body size, an effect that was not observed among males. Like in the present study, Nasir et al. (2019) highlighted an increase of queen production when rearing temperature increased from 24 °C to 30 °C. Although we observed a similar trend, the absolute number of queens produced was much lower in our colonies, suggesting that the pace of queen production was slower and that additional weeks of colony development could
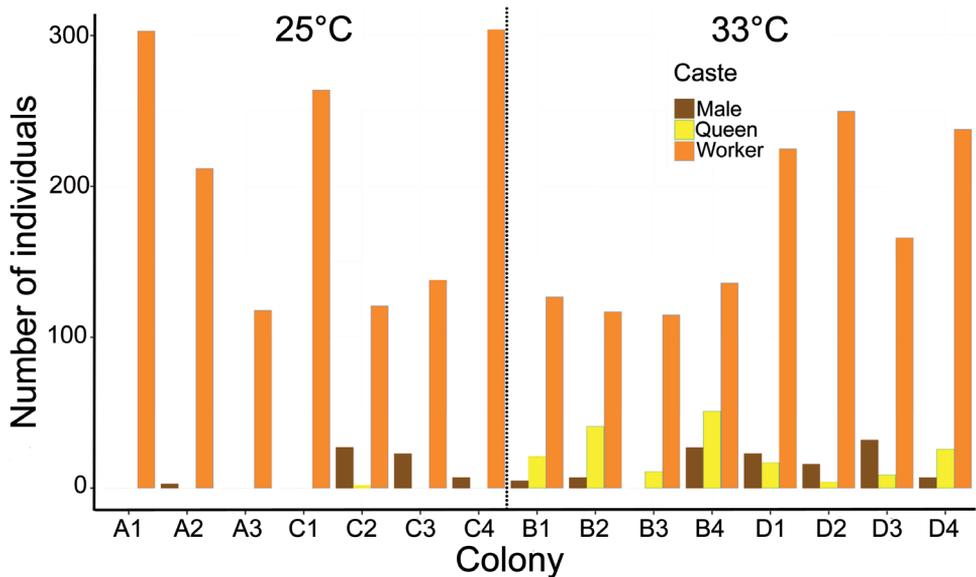
Figure 1. The effect of temperature on the total number of individuals of each caste produced in each colony Colonies A1-A3 and B1-B4 were from session 1, colonies C1-C4 and D1-D4 were from session 2. No significant effect of the session for any caste (p > 0.05). No significant impact of the temperature on the total number of individuals (p = 0.96), neither on the number of males (p = 0.24) or workers (p = 0.34) The number of queens produced was significantly higher at 33°C (p = 0.001).

have increased the total number of sexuals. In contrast with our findings, Nasir et al. (2019) found that queen production decreased at 32 °C. The higher investment in the production of queens in warmer conditions may counteract the detrimental impacts of high stressful temperatures during punctual events like heat waves. Indeed, if the mortality of bumblebees increases during prolonged periods of excessively hot weather (Rasmont and Iserbyt, 2012), higher queen production may increase the probability of a population to have successful colonies at the next generation. Our results on male and worker production are consistent with previous studies that exposed colonies to more optimal rearing temperatures. Gurel and Gosterit (2008) did not find any significant impact of temperature (*i.e.* 24 °C, 27°C and 30 °C) on worker production, and neither did Yoon et al. (2002) which used 23 °C, 27°C and 30 °C. Our findings add to this body of work by showing that the number of workers/males produced also seems relatively constant even at higher, more stressful temperatures. In addition, in our study, the queen production was also advanced at the higher developmental temperature, starting several weeks before the colonies reared at 25 °C. This is congruent with the results of Nasir et al. (2019) which also find the shortest queen emergence time at the higher temperature. This switch point is a key event during bumblebee life cycle: it marks the investment transition from growth of the colony (*i.e.* worker production) to reproduction (*i.e.* queen and male production; Lopez-Vaamonde et al. 2009). It is known that climate change is already advancing the phenology of a lot of bee species
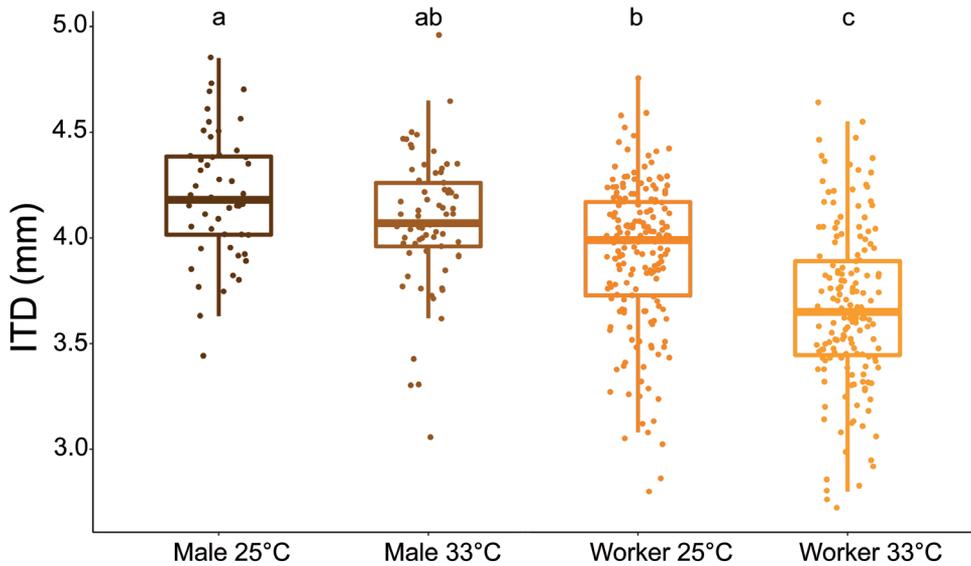
Figure 2. The impact of developmental temperature on bumblebee body size. Letters at the top of the boxplots indicate significant differences when the letters are different.

(Duchenne et al. 2020), notably bumblebee queens (Pawlikowski et al. 2020). If our results in controlled conditions can be translated the field, and if the queen production of social species also advances, we may observe an increase of voltinism (*i.e.* number of generations per year) with increasing temperature, as has already been observed in some Mediterranean regions (Rasmont et al. 2005).

As with previous studies (Atkinson 1994; Angilletta and Dunham 2003), we observed a decrease of body size at the higher developmental temperature. Among ectotherms, the decrease of body size in warmer developmental temperatures is known as the temperature-size rule and is a widespread plastic response in controlled conditions. However, as bumblebees are partly endotherms, they have the potential to buffer these changes to some extent though behavioural adaptations, such as fanning. Very little work has been done to specifically assess the impact of rearing temperature on bee body size. In one of the only studies on the topic, Gérard et al. (2018) found that, at high temperature, the centroid size of the wings (*i.e.* a proxy of wing size, often correlated with body size) was smaller, although the measurements in this study were only done on males and in very small colonies containing only few workers and some males. Thus, in contrast to our study, these colonies did not have the possibility to thermoregulate. Our results suggest that the effect of higher developmental temperatures was not balanced by the thermoregulation of workers, leading to the smaller body size of emerging workers. This decrease of body size could have potential adverse effects on the food-collecting capabilities of a colony, as it is known that bee body size can be positively correlated to foraging distance (Greenleaf et al. 2007; Kendall et al. 2019) and the mass of the pollen load (O'Neill et al. 2011; Murua 2020).

Conclusion

Our study brings us one step closer to understanding the impact that global warming may have on bumblebee colony production and individual body size. Our findings contribute to the existing body of evidence that higher developmental temperatures lead to a higher production of queens with earlier emergence times. This may represent an emergency-state of the colony where stressful conditions induced by high temperature, leading to increased fanning of workers and to a higher/earlier investment in reproduction and the success of further generations. Further studies should first try to replicate this experiment, as few studies have focussed on the impact of heat stress on life history traits, but also because working with full colonies is time-consuming and makes it difficult to have many replicates in the same experimental session. Finally, further research should also focus on how this interplay between colony production and body size could ultimately affect the efficiency with which a colony can collect resources and pollinate.

Acknowledgments

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