



**HAL**  
open science

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

Marie Guiraud, Bérénice Cariou, Maxime Henrion, Emily Baird, Maxence Gérard

### ► To cite this version:

Marie Guiraud, Bérénice Cariou, Maxime Henrion, Emily Baird, Maxence Gérard. Higher developmental temperature increases queen production and decreases worker body size in the bumblebee *Bombus terrestris*. *Journal of Hymenoptera Research*, 2021, 88, pp.39 - 49. 10.3897/jhr.88.73532 . hal-03526051

**HAL Id: hal-03526051**

<https://hal.sorbonne-universite.fr/hal-03526051v1>

Submitted on 14 Jan 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Marie Guiraud<sup>1\*</sup>, Bérénice Cariou<sup>1,2\*</sup>, Maxime Henrion<sup>1,3\*</sup>,  
Emily Baird<sup>1</sup>, Maxence Gérard<sup>1</sup>

**1** INSECT Lab, Division of Functional Morphology, Department of Zoology, Stockholm University, Svante Arrhenius väg 18b, 11418, Stockholm, Sweden **2** Sorbonne Université, Faculté des Sciences et Ingénierie, 5 place Jussieu, 75005, Paris, France **3** Ecole Normale Supérieure de Lyon, 15 parvis René Descartes, Lyon, France

Corresponding author: Maxence Gérard ([Maxence.gerard@zoologi.su.se](mailto:Maxence.gerard@zoologi.su.se))

Academic editor: Jack Neff | Received 9 September 2021 | Accepted 19 October 2021 | Published 30 December 2021

<http://zoobank.org/E40A6966-CF3A-4B44-A0A9-629C1A1028CE>

**Citation:** Guiraud M, Cariou B, Henrion M, Baird E, Gérard M (2021) Higher developmental temperature increases queen production and decreases worker body size in the bumblebee *Bombus terrestris*. Journal of Hymenoptera Research 88: 39–49. <https://doi.org/10.3897/jhr.88.73532>

## 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

\* These authors contributed equally to this work.

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.

### Keywords

Bees, climate change, colony development, ITD, Hymenoptera

## 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 21<sup>st</sup> 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-Struttman 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

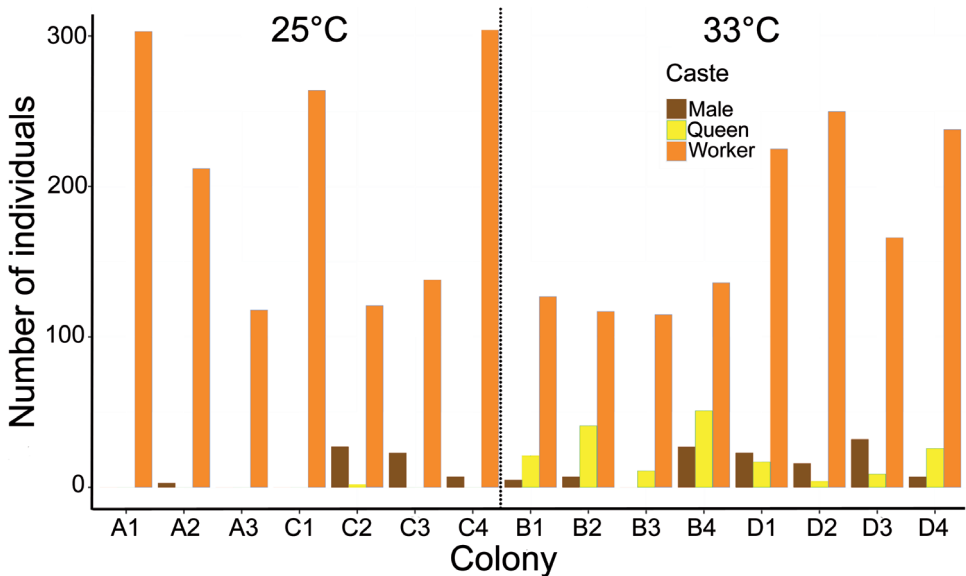
First, the session did not have any significant impact on any parameter of the colony development (all  $p$ -values  $> 0.05$ ). The temperature treatment did not affect the total number of individuals ( $p = 0.96$ ), males ( $p = 0.24$ ) or workers ( $p = 0.34$ ) produced by each colony (Fig. 1). However, 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.

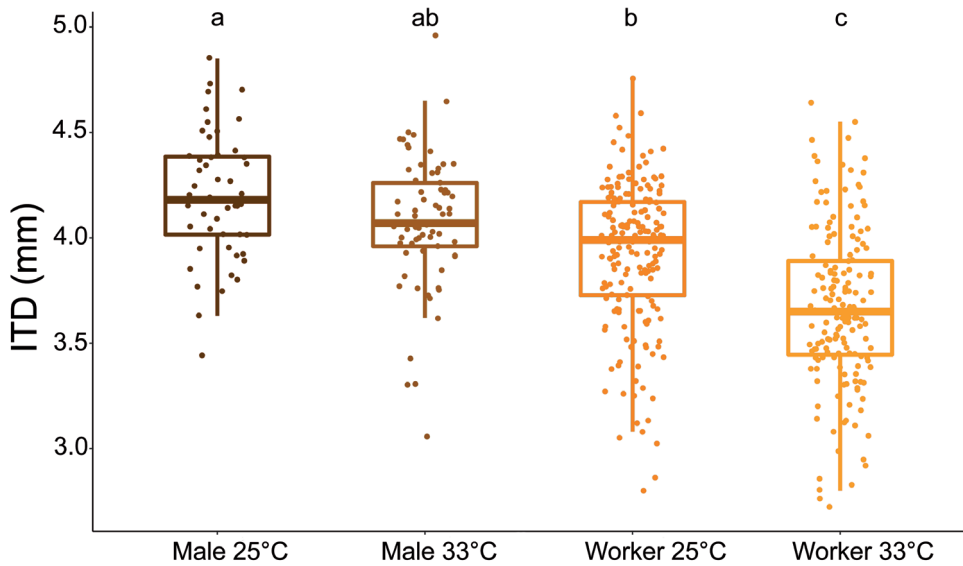
## Discussion

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

This work was supported by an Interdisciplinary Research Environment Grant from the Swedish Research Council (grant number 2018-06238). MGe was also supported by a Visiting Postdoctoral Researcher Grant from the Wenner-Gren Foundation.

## References

- Altermatt F (2010) Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences* 277: 1281–1287. <https://doi.org/10.1098/rspb.2009.1910>
- Angilletta MJ, Dunham AE (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *The American Naturalist* 162: 332–342. <https://doi.org/10.1086/377187>
- Atkinson D (1994) Temperature and organism size - a biological law for ectotherms? *Advances in Ecological Research* 25: 1–58. [https://doi.org/10.1016/S0065-2504\(08\)60212-3](https://doi.org/10.1016/S0065-2504(08)60212-3)
- Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, et al. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8: 1–16. <https://doi.org/10.1046/j.1365-2486.2002.00451.x>
- Buckley LB, Arakaki AJ, Cannistra AF, Kharouba HM, Kingsolver JG (2017) Insect development, thermal plasticity and fitness implications in changing seasonal environments. *Integrative and Comparative Biology* 57: 988–998. <https://doi.org/10.1093/icb/ixc032>
- Duchenne F, Thébault E, Michez D, Gérard M, Devaux C, Rasmont P, Vereecken NJ, Fontaine C (2020) Long-term effects of global change on occupancy and flight period of wild bees in Belgium. *Global Change Biology* 26: 6753–6766. <https://doi.org/10.1111/gcb.15379>

- Edwards M (2006) Over-wintering bumblebee in 2005/6. BWARS News-letter.
- Farmer S (2006) Over-wintering success of *Bombus terrestris* in Windsor Great Park. BWARS Newsletter, pp. 21–22.
- Gérard M, Michez D, Debat V, Fullgrabe L, Meeus I, Piot N, Sculfort O, Vastrade M, Smaghe G, Vanderplanck M (2018) Stressful conditions reveal decrease in size, modification of shape but relatively stable asymmetry in bumblebee wings. *Scientific Reports* 8: e15169. <https://doi.org/10.1038/s41598-018-33429-4>
- Gérard M, Vanderplanck M, Wood T, Michez D (2020) Global warming and plant-pollinator mismatches. *Emerging Topics in Life Sciences* 4: 77–86. <https://doi.org/10.1042/ETLS20190139>.
- Goulson D (2010) Bumblebees, behaviour, ecology and conservation (p. 336). Oxford University Press.
- Grad J, Gradisek A (2018) Bumblebee Brood Temperature and Colony Development: A Field Study. *Acta Entomologica Slovenica* 26: 219–232.
- Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecologia* 153: 598–596. <https://doi.org/10.1007/s00442-007-0752-9>
- Gurel F, Gosterit A (2008) Effects of temperature treatments on the bumblebee (*Bombus terrestris* L.) colony development Akdeniz Üniversitesi Ziraat Fakültesi Dergisi 21: 75–78. <https://doi.org/10.1016/j.agec.2015.12.007>
- Hamann E, Blevins C, Franks SJ, Jameel MI, Anderson JT (2020) Climate change alters plant-herbivore interactions. *New Phytologist* 229: 1894–1910. <https://doi.org/10.1111/nph.17036>.
- Hart AF, Maebe K, Brown G, Smaghe G, Ings T (2021) Winter activity unrelated to introgression in British bumblebee *Bombus terrestris audax*. *Apidologie*, 52: 315–327. <https://doi.org/10.1007/s13592-020-00822-w>
- Hegland SJ, Nielsen A, Lazaro A, Bjerknes AL, Totland O (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12: 184–195. <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- Kammerer M, Goslee SC, Douglas MR, Tooker JF, Grozinger CM (2020) Wild bees as winners and losers: Relative impacts of landscape composition, quality, and climate. *Global Change Biology* 27: 1250–1265. <https://doi.org/10.1111/gcb.15485>
- Klein S, Pasquaretta C, Barron AB, Devaud J-M, Lihoreau M (2017) Inter-individual variability in the foraging behaviour of traplining bumblebees. *Scientific Reports* 7: e4561. <https://doi.org/10.1038/s41598-017-04919-8>
- Holland JG, Guidat FS, Bourke AFG (2013) Queen control of a key life-history event in a eusocial insect. *Biology Letters* 9: e20130056. <https://doi.org/10.1098/rsbl.2013.0056>
- Holland JG, Bourke AFG (2015) Colony and individual life-history responses to temperature in a social insect pollinator. *Functional Ecology* 29: 1209–1217. <https://doi.org/10.1111/1365-2435.12480>
- Kendall LK, Rader R, Gagic V, Cariveau DP, Albrecht M, Baldock KCR, Freitas BM, Hall M, Holzschuh A, Molina FP, Morten JM, Pereira JS, Portman ZM, Roberts SPM, Rodriguez J, Russo L, Sutter L, Vereecken NJ, Bartomeus I (2019) Pollinator size and its conse-

- quences: Robust estimates of body size in pollinating insects. *Ecology and Evolution* 9: 1702–1714. <https://doi.org/10.1002/ece3.4835>
- Lopez-Vaamonde C, Raine NE, Koning JW, Brown RM, Pereboom JJM, Ings TC, O Ramos-Rodriguez O, Jordan WC, Bourke AFG (2009) Lifetime reproductive success and longevity of queens in annual social insect. *Journal of Evolutionary Biology* 22: 983–996. <https://doi.org/10.1111/j.1420-9101.2009.01706.x>
- Miller-Struttman NE, Geib JC, Franklin JD, Kevan PG, Holdo RM, Ebert-May D, Lynnjesica AM, Hedrick AK, Galen C (2015) Functional mismatch in a bumble bee pollination mutualism under climate change. *Science* 349: 1541–1544. <https://doi.org/10.1126/science.aab0868>
- Murua M (2020) Different Pollinators' Functional Traits Can Explain Pollen Load in Two Solitary Oil-Collecting Bees. *Insects* 11: e685. <https://doi.org/10.3390/insects111100685>
- Nasir M, Mohsan A-u, Ahmad M, Saeed S, Aziz MA, Imran M, et al. (2019) Effect of Different Temperatures on Colony Characteristics of *Bombus terrestris* (Hymenoptera: Apidae). *Pakistan Journal of Zoology* 51: 1315–1322.
- O'Neill KM, O'Neill RP, Kemp WP, Delphia CM (2011) Effect of temperature on post-wintering development and total lipid content of Alfalfa Leafcutting Bees. *Environmental Entomology* 40: 917–930. <https://doi.org/10.1603/EN10320>
- Pachauri RK, Allen MR, Barros VR, Broome J, Cramer W, Christ R, et al. (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. Geneva: IPCC.
- Pawlikowski T, Sparks TH, Olszewski P, Pawlikowski K, Rutkowski L, Jakubowski R (2020) Rising temperatures advance the main flight period of *Bombus* bumblebees in agricultural landscapes of the Central European Plain. *Apidologie* 51: 652–663. <https://doi.org/10.1007/s13592-020-00750-9>
- Perkins-Kirkpatrick SE, Lewis SC (2020) Increasing trends in regional heatwaves. *Nature Communications* 11: 3357. <https://doi.org/10.1038/s41467-020-16970-7>.
- Pylke GH, Thomson JD, Inouye DW, Miller TJ (2016) Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. *Ecosphere* 7: e01267. <https://doi.org/10.1002/ecs2.1267>
- Radmacher S, Strohm E (2010) Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). *Apidologie* 41 : 169–177. <https://doi.org/10.1051/apido/2009064>
- Rasmont P, Iserbyt S (2012) The bumblebees Scarcity Syndrome : Are heat waves leading to local extinction of bumblebees (Hymenoptera : Apidae : *Bombus*) ? *Annales de la Société Entomologique de France* 48 : 275–280. <https://doi.org/10.1080/00379271.2012.10697776>
- Rasmont P, Regali A, Ings TC, Lognay G, Baudart E, Marlier M, Delcarte E, Viville P, Marot C, Falmagne P, Verhaeghe J-C, Chittka L (2005) Analysis of pollen and nectar of *Arbutus unedo* as a food source for *Bombus terrestris* (Hymenoptera: Apidae). *Journal of Economic Entomology* 98 : 656–663. <https://doi.org/10.1603/0022-0493-98.3.656>
- Rasmont P, Coppée A, Michez D, De Meulemeester T (2008) An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). *Annales de la Société Entomologique de France* 44 : 243–250. <https://doi.org/10.1080/00379271.2008.10697559>

- Soroye P, Newbold T, Kerr J (2021) Climate change contributes to widespread declines among bumble bees across continents. *Science* 367: 685–688. <https://doi.org/10.1126/science.aax8591>
- Spaethe J, Weidenmüller A (2002) Size variation and foraging rate in bumblebees (*Bombus terrestris*). *Insectes Sociaux* 49: 142–146. <https://doi.org/10.1007/s00040-002-8293-z>
- Thibeault JM, Seth A (2014) Changing climate extremes in the Northeast United States: Observations and projections from CMIP5. *Climatic Change* 127: 273–287. <https://doi.org/10.1007/s10584-014-1257-2>
- Vogt FD (1986) Thermoregulation in bumblebee colonies I. Thermoregulatory versus Brood-Maintenance Behaviors during Acute Changes in Ambient Temperature. *Physiological Zoology* 59: 55–59. <https://doi.org/10.1086/physzool.59.1.30156090>
- Weidenmüller A, Kleinedam C, Tautz J (2002) Collective control of nest climate parameters in bumblebee colonies. *Animal Behaviour* 63: 1065–1071. <https://doi.org/10.1006/anbe.2002.3020>
- Wilson EO (1985) The sociogenesis of insect colonies. *Science* 228: 1489–1495. <https://doi.org/10.1126/science.228.4707.1489>
- Yoon HJ, Kim SE, Kim YS (2002) Temperature and humidity favorable for colony development of the indoor-reared bumblebee, *Bombus ignitus*. *Applied Entomology and Zoology* 37: 419–423. <https://doi.org/10.1126/science.228.4707.1489>.