Peer Community In Zoology

Precision and accuracy of honeybee thermoregulation

Michael Lattorff *based on peer reviews by* ***Christopher Mayack*** *and* ***Jakob Wegener***

Ugoline Godeau, Maryline Pioz, Olivier Martin, Charlotte Rüger, Didier Crauser, Yves Le Conte, Mickael Henry, Cédric Alaux (2023) Brood thermoregulation effectivenessis positively linked to the amount of brood but not to the number of bees in honeybee colonies. EcoEvoRxiv, ver. 5, peer-reviewed and recommended by Peer Community in Zoology. https://doi.org/10.32942/osf.io/9mwye

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The Western honeybee, *Apis mellifera* L., is one of the best-studied social insects. It shows a reproductive division of labour, cooperative brood care, and age-related polyethism. Furthermore, honeybees regulate the temperature in the hive. Although bees are invertebrates that are usually ectothermic, this is still true for individual worker bees, but the colony maintains a very narrow range of temperature, especially within the brood nest. This is quite important as the development of individuals is dependent on ambient temperature, with higher temperatures resulting in accelerated development and vice versa. In honeybees, a feedback mechanism couples developmental temperature and the foraging behaviour of the colony and the future population development (Tautz *et al*., 2003). Bees raised under lower temperatures are more likely to perform in-hive tasks, while bees raised under higher temperatures are better foragers. To maintain optimal levels of worker population growth and foraging rates, it is adaptive to regulate temperature to ensure optimal levels of developing brood. Moreover, this allows honeybees to decouple the internal developmental processes from ambient temperatures enhancing the ecological success of the species.

In every system of thermoregulation, whether it is endothermic under the utilization of energetic resources as in mammals or the honeybee or ectothermic as in lower vertebrates and invertebrates through differential exposure to varying environmental temperature gradients, there is a need for precision (low variability) and accuracy (hitting the target temperature). However, in honeybees, the temperature is regulated by workers through muscle contraction and fanning of the wings and thus, a higher number of workers could be better at achieving precise and accurate temperature within the brood nest. Alternatively, the amount of brood could trigger responses with more brood available, a need for more precise and accurate temperature control.

The authors aimed at testing these two important factors on the precision and accuracy of within-colony temperature regulation by monitoring 28 colonies equipped with temperature sensors for two years (Godeau *et al*., 2023).

They found that the number of brood cells predicted the mean temperature (accuracy of thermoregulation). Other environmental factors had a small effect. However, the model incorporating these factors was weak in predicting the temperature as it overestimated temperatures in lower ranges and underestimated temperatures in higher ranges. In contrast, the variability of the target temperature (precision of thermoregulation) was positively affected by the external temperature, while all other factors did not show a significant effect. Again, the model was weak in predicting the data. Overall colony size measured in categories of the number of workers and the number of brood cells did not show major differences in variability of the mean temperature, but a slight positive effect for the number of bees on the mean temperature.

Unfortunately, the temperature was a poor predictor of colony size. The latter is important as the remote control of beehives using Internet of Things (IoT) technologies get more and more incorporated into beekeeping management. These IoT technologies and their success are dependent on good proxies for the control of the status of the colony. Amongst the factors to monitor, the colony size (number of bees and/or amount of brood) is extremely important, but temperature measurements alone will not allow us to predict colony sizes. Nevertheless, this study showed clearly that the number of brood cells is a crucial factor for the accuracy of thermoregulation in the beehive, while ambient temperature affects the precision of thermoregulation. In the view of climate change, the latter factor seems to be important, as more extreme environmental conditions in the future call for measures of mitigation to ensure the proper functioning of the bee colony, including the maintenance of homeostatic conditions inside of the nest to ensure the delivery of the ecosystem service of pollination.

References:

Godeau U, Pioz M, Martin O, Rüger C, Crauser D, Le Conte Y, Henry M, Alaux C (2023) Brood thermoregulation effectiveness is positively linked to the amount of brood but not to the number of bees in honeybee colonies. EcoEvoRxiv, ver. 5 peer-reviewed and recommended by Peer Community in Zoology. https://doi.org/10.32942/osf.io/9mwye

Tautz J, Maier S, Claudia Groh C, Wolfgang Rössler W, Brockmann A (2003) Behavioral performance in adult honey bees is influenced by the temperature experienced during their pupal development. PNAS 100: 7343–7347. https://doi.org/10.1073/pnas.1232346100

Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.32942/osf.io/9mwye
Version of the preprint: 4

Authors' reply, 03 April 2023

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Decision by Michael Lattorff, posted 06 March 2023, validated 08 March 2023

minor revisions

Dear Authors,

both reviewers, who also reviewed the first version, are happy with the changes and recommend publication. However, one of the reviewers requests for some minor changes. Thus, I request that you address these before the manuscript can be fully recommended.

Kind regards

Michael Lattorff

Reviewed by Christopher Mayack, 02 March 2023

The authors have addressed all of my concerns regarding this manuscript.

Reviewed by Jakob Wegener, 01 March 2023

The authors have made considerable efforts to improve the manuscript, like the removal of zero-brood-cases from analyses of homeostasis "efficiency". It is also positive that the focus has been shifted more to the question of automated monitoring of colony strength via temperature stability. However, the authors still fail to acknowledge that this question can never be resolved (or even seriously been approached) by studying a single set of colonies in a single location. It seems evident to me that size-related differences in colony stress resilience, if they eist, will be high if there actually IS (significant) stress, and low if this is not the case.

I am also not quite convinced that the way in which the data was analysed is optimally fitted to the hypotheses to be studied. For instance, as stated before, mean brood temperature as such is not a suitable indicator of the "efficiency" of thermoregulation, at least if a linear relationship is expected, because it can be both, too high or too low. Another problem may be that most differences of colony size within the dataset are apparently linked, well, to colonies, and "colony" is used as a random variable in the dataset for modelling alongside with colony size, so that only the variation stemming from size fluctuations within colonies remains to be modelled. Also, one of the main conclusions, "efficiency" of thermoregulation is unrelated to number of bees, seems to be contradicted by one of the figures (figure 5). It is possible that bee-rich colonies were slightly warmer only because on average, they probably also contained more brood, but an indirect relationship is also a relationship.

Nevertheless, I think that the data themselves are interesting, though representative of one apiary only. Therefore, I suggest to support publication, Maybe the authors would like to use some of the comments below to further improve their data analysis.

Abstract: „efficiency" means number of units gained by number of units invested, which is not what ws measured here – maybe call it "accuracy and stability"?

L35: replace brood "size" by "amount"

L45: remove "their"

L70: "another" is not quite the right word here, because within-cell heating presumably also involves flight muscle contractions.

L81: I do not quite understand why you use mean temperature here, and not "difference between mean brood temperature and the supposed optimum for brood development"? Given that it is pupae who are most stenothermic (around 35°C), and brood nest usually contain at least some pupae, and none of the other bood stages suffer at 35°C, why not use "mean minus 35" as your indicator of "efficiency" (accuracy)?

L99 – 104: I do not understand the difference between study goals 1 (investigate whether efficiency depends on colony size) and 2 (investigate whether mean brood temp and stability depend on colony size)- as you write in the abstract that you use mean brood temp and stability as proxies of "efficiency"

L108: "without needing more data such as climate data" – given that your data stems from one location (and one climate) only, how could you possibly verify this hypothesis? If, for instance, you would find no relationship between colony size and "efficiency" under a climate where outside temp only varies between 20 and 25 °C, would this then prove that no such relationship exists under a climate with extreme temperature changes, such as in a desert?

L125 was sensor accuracy also checked at this occasion?

L130 GB, not Go

L137: ...and contains 4.000 brood cells under the hypothesis that every cel is fille with brood

L155: replace "for" with "from"

L161: the mean temperature alone cannot be used to represent the "efficiency to the optimum brood temperature" if no reference is given (what IS the optimum brood temperature?). Please use "mean minus optimum" as your indicator

L183: Given the extreme starting variations of the size of your colonies, most of the variability of the predictor "colony size" probably was explained by the random effect "colony replicate" – in other words, your replica (measurements) were not independent (because groups of them represent repeated measurements of the same colonies) – so how could you use these data to properly address the relationship between colony size and "efficiency" of thermoregulation?

L232: you say you had no a priori reason for expecting relationships between your predictors, but isn't it clear for instance that cooling a colony by evaporation will be more difficult if temperature is high and there is precipitation (i.e. high humidity) at the same time?

L244: lacking: "so"

L278: for the reason explained above, it would be interesting to know the proportion of the variation explained by the random colony effect

L352: as you used regression, a significant effect means that the predictor has an influence on the dependent variable, not (merely) that it is correlated

L366: "We did not find that mean brood temperature significantly increases with the number of adult bees".... But your fig. 5 a shows just that! I suspect that the L376model you adjusted did not detect this relationship because most of it was absorbed by the random colony variable.

L376 I acknowledge that this is an mprovement compared to the first version of the manuscript

L405: It would be nice to have a graph depicting CV as a function of outside temp, and a description f water availability at the experimental site

L444: amount of brood

Evaluation round #1

DOI or URL of the preprint: `https://doi.org/10.32942/osf.io/9mwye`
Version of the preprint: 3

Authors' reply, 11 January 2023

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Decision by Michael Lattorff, posted 27 September 2022

major revision

Dear authors,

two experts in the field have reviewed you preprint. Both see a high value in the study, one of the reviewers is very critical about your experimental design and the sample size. You should take this criticism seriously and comment on each of the points raised and revise your manuscript accordingly.

Kind regards

Michael Lattorff

Reviewed by Jakob Wegener, 23 September 2022

The factors influencing honeybee colony thermoregulation are a topic of growing importance, because these need to be known if we are to model effects of changing climates on colonies and define strategies to breed climate-resilient stock. The present study is generally well-written (except maybe for the abstract), and the authors deploy an impressive set of statistical methods to model the efficiency of colony thermoregulation on size indicators and meteorological data. The main weakness of the study, apart from the fact that it is based on a very limited number of locations (1), colonies (39) and time points (9), is the fact that brood temperature was measured only at one – fixed - location within the colony. As the authors state themselves (L365 ff), the results they obtain (greater stability of temperature and a trend towards higher temp in stronger colonies) would also be expected under the hypothesis that the thermosensor in small colonies was frequently outside of the brood area.

A second major shortfall is that mean brood nest temperature is used as a proxy of "precision" of thermoregulation. In metrics, this term usually refers to the degree of dispersal of measurements around their mean (as opposed to accuracy, which refers to the average distance from a "true" value). In the present study, the proxy for what is termed precision is the mean temperature around the brood (line 311). This means that thermoregulation in colonies with a permanently elevated brood nest temperature would have been rated as "precise", and, according to the terminology of the study, this would have contributed to the "efficiency" of thermoregulation, even if the outside temperature would have been 40 °C, so that an efficient thermoregulatory system would be one that is able to keep the brood near its physiological optimum. In my opinion, it would have been more interesting to measure accuracy of thermoregulation, defined as the average difference from a value seen as the optimum (based on a literature review of physiological/developmental studies).

Finally, the main conclusion – colony size matters for thermoregulation and weather also plays a role – is of limited novelty and value if the numerical boundaries of brood and bees that limit the capacity of the colony to maintain developmental stability of the brood are not given, and their dependency on outside temperature, irradiation and humidity is not determined in numbers. A statement like "colonies with fewer than XY workers were unable to maintain broodnest temp within the physiologically optimum range of X – Y °C if outside temp surpassed a value of XY °C" would be more useful.

Detailed comments can be found below.

Title: a little confusing, because it suggests that numbers are stable – instead, what you mean to dsay I believe is that something (temperature) stays stable because of a number (of bees) – maybe "stability through numbers"?

Keywords: are lacking. None required for this publication platform?

L14: strictly speaking, thermoregulation means that temperature is regulated, not that it is kept stable – in the winter cluster, temp drops to values below brood rearing conditions, and still is regulated.

L19: increased efficiency of homeostasis

L19: Therefore, we determined ...

L23: temperature has no brood optimum (being able to breed temperatures would be useful in the current energy crisis, though) – replace by "temperature close to the optimum value for honeybee brood rearing"

L29: brood temperature – if you mean the temperature of brood, then this formulation is correct. If you mean the temperature at which brood rearing is possible, then you should write this.

L36-38: I do not understand why the fact that brood temperature constancy was insufficient for approximating colony size should signify that thermoregulation is flexible and efficient

L46: citation lacking

L52: is, therefore,

L55: optimum

L79: see above (L23); maybe "average deviation from the optimum brood rearing temp"?

L87: is, therefore,

L117: please indicate the subspecies/breed of bees used, as well as the size and material of hive boxes used – both may be important for thermal homeostasis

L126: for the setup t properly determine brood temperature, it is clearly essential that the sensor is at the centre of the brood nest at all times. How was this assured, if the sensor was stably installed in a given position?

L137: as this method is based on the "Liebefeld" method for measurement of colony strength, the original citation should be given here

L150: this clearly means that the sensors were outside of brood nests in some cases. So how can you guarantee that they were firmly within brood nests in those cases where the temperature amplitude was smaller? It might be that the sensor was just at the border of the brood nest, so that fluctuations observed were stronger than they might have been if measured at the centre.

L165: what was the distance between the weather station and the hives? Was the microclimate the same? Were all the hives exposed to sunlight to the same degree?

L190: please explain what an "identity link" function is

L226: you state that you had no a priori-reason for considering predictor interactions – what about the well-known fact that both mean temp and stability of homeostasis drop in the absence of brood? There were also cases with 0 brood cells in the dataset...

L242: the latter

L245: were individual measurements or colonies used as replicates here (n=29 or n=236)? Please indicate in the main text and not in the appendix

Fig. 1, caption: please explain abbreviations used for predictors in the figure caption. What is meanS – shouldn't this be meanTS?

Fig.2: Seems like the model systematically overestimated the effects – doesn't this mean that something went wrong with model adaptation?

L329: apparently there is a problem with a text mark here

Methods: it would be good to mention the boundaries of the classes of bees and brood in the main text – this information is important to interpret the results

L340: regression analysis is adequate if a cause-and-effect – relationship is to be studied... but is it realistic to use temperature as the explanatory variable here? I would expect that the efficiency of thermoregulation would be increased by the colony as a consequence of the presence of brood, not vice versa.

L360 ff: this sentence does not seem tomake sense to me – does the likelihood of the individual to respond to a stimulus not in itself depend on the the intensity of the stimulus?

L385-87: stated like this, the fact that weak colonies have a reduced capacity to thermoregulate is a banality. For your analysis to make sense, it would be necessary to discuss the boundary of the number of bees underneath which thermoregulation reaches a level of instability that could become detrimental to brood development. As this boundary likely depends on the level of irradiation and outside temp, the critical threshold values of irradiation, outside temp and outside humidity (limiting the capacity to cool through evaporation) should be assessed.

L424: an alternative explanation for this is would be that temperatures usually drop when there is precipitation, and heat may be the bigger challenge to temp stability than cold during the summer

Reviewed by Christopher Mayack, 12 September 2022

The article "Stability in numbers: a positive link between honeybee colony size and thermoregulatory efficiency around the brood" was found to be well written and well cited. The analyses were thorough that included appropriate modeling techniques. Moreover, this article addresses an interesting question of whether automated temperature monitoring systems can be used to predict colony strength in terms of brood and adult bee numbers.

Introduction

The introduction is well written and well cited.

Methods

The experimental design matches the analysis. The analyses are performed correctly. Extra steps were taken to account for random effects and multicollinearity. The data was scaled to make it comparable for model analysis. The methods are well cited.

Results

Line 330: There is an error message with one of the references to the appendix.

In figure 5, I would remove the p-values above the bars and would stick with the asterixis, it is too busy and too much information with the p-values added in.

Discussion

The interpreted results match the analysis and study design. The discussion is written concisely and is to the point. An appropriate amount of speculation is used based on the results obtained.

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