Peer Community In Zoology

Cuckoo bumblebee males might reduce plant fitness

Michael Lattorff *based on reviews by Silvio Erler, Patrick Lhomme and 2 anonymous reviewers*

A recommendation of:

Cuckoo male bumblebees perform slower and longer flower visits than free-living male and worker bumblebees

Alessandro Fisogni, Gherardo Bogo, François Massol, Laura Bortolotti, Marta Galloni *(2021), Zenodo, 10.5281/zenodo.4489066, ver. 1.2 peer-reviewed and recommended by PCI Zoology* ***https://doi.org/10.5281/zenodo.4489066***

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Recommendation

In pollinator insects, especially bees, foraging is almost exclusively performed by females due to the close linkage with brood care. They collect pollen as a protein- and lipid-rich food to feed developing larvae in solitary and social species. Bees take carbohydrate-rich nectar in small quantities to fuel their flight and carry the pollen load. To optimise the foraging flight, they tend to be flower constant, reducing the flower handling time and time among individual inflorescences (Goulson, 1999). Males of pollinator species might be found on flowers as well. As they do not collect any pollen for brood care, their foraging flights and visits to flowers might not be shaped by the selective forces that optimise the foraging flights of females. They might stay longer in individual flowers, take up nectar if needed, but might unintentionally carry pollen on their body surface (Wolf & Moritz, 2014).

Bumblebees are excellent pollinators (Goulson, 2010), and a few species are exploited commercially for their delivery of pollination services (Velthuis & van Doorn, 2006). However, a monophyletic group of socially parasitic species – cuckoo bumblebees – has evolved amongst the bumblebees, lacking a worker caste. Cuckoo bee gynes usurp nests of free-living bumblebees, kill the resident queen, and forces the host workers to rear their offspring consisting of gynes and males (Lhomme & Hines, 2019). The level of affected colonies in an area can be up to 42% (Erler & Lattorff, 2010).

The behaviour of the cuckoo bumblebees, especially that of the males, has been rarely studied. The present study by Fisogni et al. (2021) has targeted the flower-visiting behaviour of workers and males of free-living bumblebees and males of the cuckoo species. They used behavioural observations of flower-visiting insects on *Gentiana lutea*, a plant from south-eastern Europe with yellow flowers arranged in whorls. While all

three groups of bees visited the same number of plants, males of both types visited more flowers within a whorl, but cuckoo males spent more time on flowers within a whorl and the whole plant than the free-living bumblebees.

The flower visits of bumblebee workers are optimised, aiming at collecting as much pollen as possible within a short time frame. This, in turn, has consequences for the pollination process by enhancing cross-pollination between different plants. By contrast, males and especially cuckoo bumblebee males, are not selected for an optimised foraging pattern. Instead, they spend more time on flowers, eventually resulting in higher levels of pollen transfer within a plant (geitonogamy), which might lead to reduced plant fitness. This is the first study to relate the foraging behaviour of cuckoo bumblebees to pollination and plant fitness.

References

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Reviews

Toggle reviews

Reviewed by Silvio Erler, 16 Sep 2021

The authors nicely revised their manuscript by including most reviewer suggestions and addressing their concern. The point-by-point authors response sufficiently answered the reviewer concerns. I have only some minor comments that might improve the manuscript.

- I suggest to change the writing from “bumblebee” to “bumble bee”.

- Table 1 and main text: Please name the cuckoo bumble bee “Psithyrus” instead of “Bombus” to make clear that these are the cuckoo species.

Reviewed by Patrick Lhomme, 05 Sep 2021

The authors took into account the comments from all reviewers. I'm satisfied with this new version.

best regards,

Patrick

Evaluation round #1

12 May 2021

DOI or URL of the preprint: *https://doi.org/10.5281/zenodo.4489067*

Version of the preprint: 1.0

Author's Reply

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Dear Dr. Lattorff, thank you for handling our manuscript. We have addressed all the experts’ comments and modified the text accordingly. We have provided precise replies to each comment in the attached file. We have uploaded the revised version of the manuscript, supporting information and R scripts on Zenodo.

Decision by Michael Lattorff

Dear authors,

your subission was evaluated by four experts in the field. All of them were very convinced about your study and enjoyed reading your ´well written manuscript. However, they also raised some concerns about methodology and data anaylsis. I think these issues need to be addressed to improve your mansucript. Please, read all reviewer reports carefully and respond to the points raised in a point-by-point response document incl. how the points raised affected your manuscript.

Many thanks for submitting your work to PCI Zoology, we are looking forward to receiving you revision.

Reviewed by Patrick Lhomme, 14 Mar 2021

Dear authors, I have enjoyed reading your ms entitled “Cuckoo bumblebees perform slower and longer flower visits than true bumblebees”, it is a well written MS that is pleasant to read.

Males are generally considered to visit fewer flowers than workers, to be slower paced and to have a lower flower fidelity however most of the pollen they carry is freely available for pollination so I believe that their contribution to pollination services is often overlooked.

One strength of the study is to highlight this contribution and show that what we generally think about bumblebee male foraging is maybe not always true and probably more context-dependent.

Among the weakness, I feel that the authors are stretching their data a bit too much in trying to compare foraging behavior of cuckoo bumble bees and free-living bumble bees using only cuckoo male versus host

worker/male foraging data. Including data from Bombus queens and Psithyrus females would have been a plus.

Unlike Bombus queens, Psithyrus females do not forage to feed their colony but only for themselves, their incentive to forage is thus very different although both have also offspring to produce, the comparison would thus have been very interesting. I noticed that females of certain species of cuckoo bumble bees like B. vestalis are regularly observed foraging while others like B. rupestris females are rarely encountered foraging on flowers although both species population density seem pretty similar (interestingly it's opposite for males, as you show in your dataset). I believe females of B. rupestris feed directly on the resources gathered by their hosts and don't bother much foraging, so the parasitic strategy can I'm sure explain differences in foraging behaviours between cuckoo and free-living bumble bees but also between the different cuckoo species.

The comparison of both cuckoo and free-living males makes sense too, although they might have very similar physiological requirements, the parasitic strategy of the females could probably explain some the minor differences between cuckoo and free-living male foraging behaviors, as discussed by the authors. I also noticed that mating durations between cuckoo and host bumblebees were drastically different (see Lhomme et al 2013) for reasons that I can't really explain, but this could somehow impact male foraging behavior. As mating duration is almost 10 times shorter in cuckoos their energetic needs might also be much lower I don't know.

I'm also a bit frustrated not to have more qualitative data to interpret the results. You measured visiting durations but it would have been useful to measure foraging durations, it's not clear to me if the males are feeding or just resting on the flowers, quantifying resting / nectar foraging / pollen foraging would have also been a plus.

Here are some minor comments:

Title : This title is misleading, you can't really state this based on your study. You are comparing bumble bee workers with cuckoo males. It would have made sense if you were comparing Bombus queens and Psithyrus female foraging behaviors, but it's not the case here. Please provide a more accurate title or at least specify that cuckoo bumblebees are males and that true bumblebees are workers

L 26-28 : Many studies have investigated differences between cuckoo bumble bees and their hosts in terms of social behaviors, pre-mating behaviors etc... You should be more specific on the behavior (flower visiting behavior) you talk about.

Keywords : In general, avoid using words that are already in the title.. I would for example replace "cuckoo bumble bees" by Psithyrus, "behavior" is also too vague, use flower visiting behavior

L 52 : Williams 1998 actually cites 29 species, it was before Lecocq et al. (2011) show conspecificity between B. barbutellus and B. maxillosus. I don't like doing that (self citation) but we also confirmed in a recent paper (in press) that B. flavidus and B. fernaldae are conspecific, so the number of species is now 27. You can just simply stick to 28, but if you wish to specify 27 and if you're allowed to cite papers in press with DOI then feel free to cite "Lhomme P, Williams SD, Ghisbain G, Martinet B, Gérard M, Hines HH (2021) Diversification pattern of the widespread Holarctic cuckoo bumble bee Bombus flavidus (Hymenoptera : Apidae) : The East Side Story. Insect Systematics and Diversity, in press, doi: 10.1093/isd/ixab007"

L. 56 : To be honest I'm not a big fan of the adjective "true" to refer to non-parasitic bumblebees, Psithyrus species are also true bumble bees.. I would rather use the terms "cuckoo vs free-living" or "cuckoo vs host", but it's just a personal preference feel free to keep "true" if you wish.

L. 211-214 : I agree but it doesn't really make sense here. If you were comparing bumblebee queens and cuckoo females I would agree but here you compare workers versus males, the parasitic behavior of females has nothing to do with male flower visiting behavior.

L. 271 : were cuckoo bumblebee male**s**.

Best wishes,

Patrick Lhomme

Reviewed by anonymous reviewer, 06 Apr 2021

Fisogni and co-authors present an interesting study comparing behavior of cuckoo and free-living bumblebees. They studied floral visit of different individuals on patches of Gentiana lutea and they show that behaviors are different. We need more empirical studies like this one to better understand the ecology of the pollinators, and their conservation. I recommend the publication of this article but I present here different propositions to make the presentation of this study more accurate.

Change everywhere in the manuscript the term “true bumblebees”, including in the title. As you know, Psithyrus are now included in the genus Bombus. I recommend to use the term “free-living bumblebees” or “non-parasitic” if you want to distinguish the cuckoo bumblebees with the other bumblebees.

You have to include in the abstract and in the introduction the interest of your study. Why is it important to compare the two groups? Why is it important to compare their behavior? What’s your hypothesis? You should indicate, in the abstract and in the introduction, that the evaluation of the behavior during the floral visit is important to estimate the efficiency of a pollinator and its fitness. We might think that the cuckoo bees are not good pollinators because they don’t forage on pollen.

Line 34: Significant differences?

Line 37; Lines 239-241: I did not understand this mechanistic hypothesis to explain the different behavior by the difference in colony development. Where are the data on the timing of colony development? What about other traits like the size? The physiological needs? The flight metabolism?

Lines 51-53: evolution of inquilinism in 3 subgenera (see Lhomme & Hines 2019)

Lines 65-67: to be developed. What makes a pollinator efficient or not? Cleaning behavior for exemple should be introduced. Pollen on corbiculae is not available for pollination.

Line 90: size of the flower?

Line 94: Rossi et al. 2014 did not explore the present question?

Line 108: How did you determine the species in the field?

Line 128: why you don’t consider species level? Difference among free-living bumblebees species might be more important than between cuckoo versus free-living forms. I would test first differences at species level, and if you don’t have differences, you can pool the data. Aggregation of data has to be justified.

Line 156. Table 1: The subgenus system presented here is outdated. Please follow Williams et al. 2008. All cuckoo species listed here are included in the subgenus Psithyrus.

Williams P.H., Cameron S.A., Hines H.M., Cederberg B. & Rasmont P. (2008) A simplified subgeneric classification of the bumblebees (genus Bombus). Apidologie, 39, 46-74

Line 161. There is no justification to lump the data from different species. In other words, are the differences related to species or to “trait” (cuckoo versus free-living)?

Line 167. The accuracy to study these metrics was not introduced.

Lines 204-205; lines 216-217. If it’s not significant, don’t mention it. It does not make sense.

Line 247: Please clarify. How?

Reviewed by anonymous reviewer, 28 Feb 2021

This is an nice example of rare studies asking the relevance and importance of bumble bee males for pollination and plant reproductive success. In particular socially parasitic cuckoo bumble bees are completely neglected in this context. Here, the authors found that cuckoo males stay much longer on flowers and behave slower than host bumble bee workers and males, most likely related to the different foraging strategies and colony development.

The study design, data analysis and presentation is clear and easy to follow. The authors use all relevant literature to discuss and explain their data. However, a major downside of the study is the very limited observation time with only 3 days per year (6 in total). It is well known that climate (temperature, hours of sunshine, rain, etc.) significantly impact flower nectar production and bumble bee foraging behaviour. It is needed to include climate data during observation to discuss the pros and cons of the data. Slower behaviour and resulting longer flower visits might also be explained by the climate data, this discussion is missing so far.

It might also be worth separating data for the host bumble bee species, having a huge difference between sexes for B. terrestris, B. lapidarius and B. pratorum. For each species, colony life cycles differ strongly among months and might be included in the discussion of the data.

The efficiency of pollination success can be easily supported by having pollen data of the foraging bees. Did the authors count pollen grains per cuckoo and host bumble bee males and workers while foraging?

Table 2 and 3 might move to the suppl. material.

Line 208-214: Is there anything known on nectar and pollen quality, nutritional values, of G. lutea. If yes, this would be relevant for the discussion on energy intake and foraging behaviour strategies.

Line 216-223: Seems to be redundant compared to previous sections and should be shortened. Generally, the authors should double-check for redundancy between the introduction and discussion.

The authors highlighted several times that only males of cuckoo bumble bees have been found, but no queens. Do they have any data that at the same time queens were foraging on other plants in the same vicinity and that young queens already emerged? Otherwise I would reduce the discussion on this fact.

Reviewed by anonymous reviewer, 06 Apr 2021

In general, it's a well written and interesting manuscript. I do see a few areas where the ms could be improved and clarified.

Methods

Line 110: the authors verify visual identification by capturing and keying out species after visual surveying the visitations. My concern here is that this approach will validate the experimenter's eye for identifying species/sex but not whether they were successful in the instance of observation. IDing the bees while visiting plants is absolutely achievable by experienced observers but it's not always trivial and especially when they're moving around and have their head buried in a flower etc. For example, B. terrestris males look largely similar to females but have a different 'face'. Being confident in sexing can require a close look.

Stats: I think that some mention of species variation in foraging is warranted. I have gone through their well annotated code and included bumblebee species. In none of the models I tried did bumblebee species significantly explain the response variables. This then makes it sensible to ignore, but it should be mentioned explicitly in text that they did not vary by species (unless I missed something).

I do find, however, some issue with two things. First, I suspect that a generalized linear model would be more appropriate for the number of flowers/whorls visited with a Poisson error distribution (or quasi if

overdispersed). Second, some of thse counts seem to have quite a bit of missing data (NAs) in the data file. More explanation of thse missing data should be provided.

How well do these correspond with individual identifications. I find it a bit hard to connect the two. When recording visits on a plant, one has to make spot judgements. The sampling afterwards would help confirm your confidence of identification in general but wont actually validate your decision at the time. For the species here, it is pretty straightforward to distinguish. But, for identifying sex it can be trickier. For eg. B. terrestris males look very similar to females. People with experience can vey reliably identify which are males and females (and I'm sure you are) but it relies on a clear view of the bee, and in particular, their head (which can be obscured if it's deep in a a flower).

Discussion.

L235 is an interesting suggestion, that phenology determines foraging activity. This is intuitive. A correlate of this is that the bees differ in age. If sexuals are produced earlier for cuckoo bumblebees then we would expect them to be older on average than the other bumblebees. This could be estimated by wing wear from the collected samples.

L241 this would be supported by phenology data.