Peer Community In Evolutionary Biology

# Maternal effects in sex-ratio adjustment

***Dries Bonte*** *based on peer reviews by 2 anonymous reviewers*

Alison B. Duncan, Cassandra Marinosci, Céline Devaux, Sophie Lefèvre, Sara Magalhães, Joanne Griffin, Adeline Valente, Ophélie Ronce, Isabelle Olivieri (2018) Transgenerational cues about local mate competition affect offspring sex ratios in the spider mite Tetranychus urticae. bioRxiv, ver. 3, peer-reviewed and recommended by Peer Community in Evolutionary Biology. 10.1101/240127

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Optimal sex ratios have been topic of extensive studies so far. Fisherian 1:1 proportions of males and females are known to be optimal in most (diploid) organisms, but many deviations from this golden rule are observed. These deviations not only attract a lot of attention from evolutionary biologists but also from population ecologists as they eventually determine long-term population growth. Because sex ratios are tightly linked to fitness, they can be under strong selection or plastic in response to changing demographic conditions. Hamilton [1] pointed out that an equality of the sex ratio breaks down when there is local competition for mates. Competition for mates can be considered as a special case of local resource competition. In short, this theory predicts females to adjust their offspring sex ratio conditional on cues indicating the level of local mate competition that their sons will experience. When cues indicate high levels of LMC mothers should invest more resources in the production of daughters to maximise their fitness, while offspring sex ratios should be closer to 50:50 when cues indicate low levels of LMC. In isolated populations, Macke et al. [2] found sex ratio to evolve fast in response to changes in population sex-structure in the spider mite *Tetranychus urticae*. Spider mites are becoming top-models in evolutionary biology because of their easy housekeeping, fast generation times and well-studied genome [3]. The species is known to respond fast to changes in relatedness and kin-structure by changing its mating strategy [4], but also dispersal [5]. Sex ratio adjustments are likely mediated by differential investments in egg size, with small eggs possibly experiencing lower chances of fertilization, and thus to develop in haploid males [4]. Alison Duncan and colleagues [6] asked the question whether sex ratios change plastically in response to changes in the local population structure. They additionally questioned whether maternal effects could drive changes in sex-allocation of spider mite mothers. Indeed, theory predicts that if environmental changes are predictable across generations, intergenerational plasticity might be more adaptive than intragenerational plasticity [7]. Especially in spatially structured and highly dynamics populations, female spider mites may experience highly variable demographic conditions from one generation to another.

During range expansions, spatial variation in local relatedness and inbreeding are documented to change and to impact eco-evolutionary trajectories as well (e.g. [8]). Duncan et al. [6] specifically investigate whether the offspring sex ratio of *T. urticae* females changes in response to 1) the current number of females in the same patch, 2) the number of females in the patches of their mothers and 3) their relatedness to their mate. They surprisingly find the maternal environment to be more important than the actual experienced sex-ratio conditions. These insights thus show the maternal environment to be a reliable predictor of LMC experienced by grand-children. Maternal effects have been found to impact many traits, but this study is the first to convincingly demonstrate maternal effects in sex allocation. It therefore provides an alternative explanation of the apparent fast evolved responses under constant demographic conditions [2], and adds evidence to the importance of non-genetic trait changes for adaptation towards changing demographic and environmental conditions.

***References:***


[1] Hamilton, W. D. (1967). Extraordinary Sex Ratios. Science, 156(3774), 477–488. doi: [10.1126/science.156.3774.477](https://dx.doi.org/10.1126/science.156.3774.477)

[2] Macke, E., Magalhães, S., Bach, F., & Olivieri, I. (2011). Experimental evolution of reduced sex ratio adjustment under local mate competition. Science, 334(6059), 1127–1129. doi: [10.1126/science.1212177](https://dx.doi.org/10.1126/science.1212177)

[3] Grbić, M., Van Leeuwen, T., Clark, R. M., et al. (2011). The genome of *Tetranychus urticae* reveals herbivorous pest adaptations. Nature, 479(7374), 487–492. doi: [10.1038/nature10640](https://dx.doi.org/10.1038/nature10640)

[4] Macke, E., Magalhães, S., Bach, F., & Olivieri, I. (2012). Sex-ratio adjustment in response to local mate competition is achieved through an alteration of egg size in a haplodiploid spider mite. Proceedings of the Royal Society B: Biological Sciences, 279(1747), 4634–4642. doi: [10.1098/rspb.2012.1598](https://dx.doi.org/10.1098/rspb.2012.1598)

[5] Bitume, E. V., Bonte, D., Ronce, O., Bach, F., Flaven, E., Olivieri, I., & Nieberding, C. M. (2013). Density and genetic relatedness increase dispersal distance in a subsocial organism. Ecology Letters, 16(4), 430–437. doi: [10.1111/ele.12057](https://dx.doi.org/10.1111/ele.12057)

[6] Duncan, A., Marinosci, C., Devaux, C., Lefèvre, S., Magalhães, S., Griffin, J., Valente, A., Ronce, O., Olivieri, I. (2018). Transgenerational cues about local mate competition affect offspring sex ratios in the spider mite *Tetranychus urticae*. BioRxiv, 240127, ver. 3. doi: [10.1101/240127](https://dx.doi.org/10.1101/240127)

[7] Petegem, K. V., Moerman, F., Dahirel, M., Fronhofer, E. A., Vandegehuchte, M. L., Leeuwen, T. V., Wybouw, N., Stoks, R., Bonte, D. (2018). Kin competition accelerates experimental range expansion in an arthropod herbivore. Ecology Letters, 21(2), 225–234. doi: [10.1111/ele.12887](https://dx.doi.org/10.1111/ele.12887)

[8] Marshall, D. J., & Uller, T. (2007). When is a maternal effect adaptive? Oikos, 116(12), 1957–1963. doi: [10.1111/j.2007.0030-1299.16203.x](https://dx.doi.org/10.1111/j.2007.0030-1299.16203.x)


## Reviews

## Evaluation round #2

DOI or URL of the preprint: **10.1101/240127**

Version of the preprint: 2

### Authors' reply, 07 June 2018

Dear Dries,

Thank you very much for your very helpful comments on our manuscript. I have just uploaded a copy of the revised pdf, with the PCI recommendation page at the front as requested. I will send you the link once it is approved. In the end I removed the text in the Discussion about how a less female biased sex ratio may be to avoid inbreeding. After re-reading the paper I don't think this is applicable to our experiment as we only had 1 female on a patch in the 'sib-mating' experiment, so no option to outbreed. Also, I think this aspect of the model is more relevant to species which do split sex ratios. I also made the majority of changes requested by the reviewer, except 2 recommendations where I think the English is wrong.

Kind regards, Alison

### Decision by Dries Bonte, posted 07 June 2018

**recommendation of your preprint: revision needed**

Dear Alison,

I obtained comments from one reviewer and read the manuscript carefully as well. As you will see, we are nearly there - this make a nice contribution to the literature on putative adaptive maternal effects.

While the reviewer comes up with some textual edits, i read it through the glasses of a non-expert audience (so to make it digestible for a wider audience) and have a few comments:

line 24: within the local, rather than isolated

lines 47-49: can you add a sentence on the reasoning, as this is an additional mechanisms not explained earlier

line 80: add 'the parasitoid wasp'

lines 303-305: needs a couple of sentences to explain

lines 394-395: but they are likely present if they recognise kin(d). From an adaptive perspective the cues from mothers should then be more reliable than those obtained directly, or allow a much faster response to avoid LMC (no lags)

Looking forward to finalise this procedure!

Dries

### Reviewed by anonymous reviewer 1, 15 April 2018

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## Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/240127

Version of the preprint: 1

### Authors' reply, 11 April 2018

**Download author's reply**

### Decision by Dries Bonte, posted 11 April 2018

**Revise**

Alison Duncan and colleagues investigated their role of maternal effects and sib mating on offspring sex-ratios. They conducted several laboratory experiments in which maternal LMC was manipulated by changing the number of founders, while maintaining density. The paper is to my opinion well written, data well analysed and collected.

The reviewers agree with my evaluation but came up with several issues that the authors want to take into account to improve their paper. While I found the reasoning regarding predictability well explained (I am also of opinion that the perspective of local information not matching cross-generationally integrated population-level information is indeed key to understand many demographic dynamics), the reviewers want to see some aspects of the reasoning better worked out. Reviewer one questions the validity of the experiments because of putative problems with the experimental setup and the used patch sizes. As a recommender of your manuscript, I believe issues on this can be avoided by providing a schematic presentation of your breeding design. Especially the descriptions on the different sample sizes (patches) in the quarters of the boxes are hard (not to say impossible) to understand since no reasoning for this setup is given. I recommend the authors to make this part clearer to the audience, as this information seems central to understand the potential drivers of the recorded maternal effects on offspring sex ratio.

In addition, the authors should provide the raw data (e.g. in supplementary material) or the link to the raw data if they are deposited on an open repository. Similarly, the authors should give more details about their statistical analysis (a SAS script would be particularly welcome). These requirements are indicated in the PCI ethical code of conduct (https://evolbiol.peercommunityin.org/about/ethics).

## Reviewed by anonymous reviewer 1, 10 January 2018

In general, this study aims to experimentally test potential cues that the spider mite, T. urticae, uses to adjust sex ratio of its offspring. I have a number of concerns or questions related to interpretation of their results. One of the important questions I have is related to patch size as actually experienced by the females under the experimental design and how that relates to typical patch size in nature. Having multiple small experimental patches located in the same box could be a problem if odor is a cue the female uses to assess presence of other females in a patch. I am also not completely convinced that inter-generational information exchange is the most parsimonious explanation for the results in Fig. 1B, especially given contradictory results in earlier studies. Detailed comments along these lines are presented below, mixed in with more minor comments.

L42: ”Furthermore ... should also select...”? compared to what? In the previous sentence, the authors simply state that sons are of less value than females in a LMC situation. It does not say why that should be. Only the sentence starting at L42 gives a reason, and that is only for haplodiploid species (i.e., mothers more related to daughters than to sons).

The authors say (l38-39) that LMC ”is expected to select for female-biased offspring sex ratios”. It would be helpful to the reader to explain what underlies that expectation; Why is it expected? Is it expected only for haplodiploid species? If not, why is it also expected in diploid species?

L65: change ”whole” to ”wide”

L72: I cannot make sense of this sentence. How can under-study of anything result in biological variation? Something is missing that would clarify the logic. Do the authors mean variation in adjustment may be related to variation in cues? Or do they mean lack of experimental control of cues results in different outcomes of adjustment between studies? Or something else?

L75: change ”in the immediate whilst” to ”while”

L79: why ”In contrast”? These just look like more examples of types of cues, not something that contrasts with the previous sentence.

L82: delete comma after ”cues”

L90: change ”this” to ”that”; otherwise it reads as if the authors are talking about their own current study, rather than the 2011 study.

L113: missing a close-parenthesis

L123: 2011a or b?

M&M: It would be helpful to have schematic figures illustrating the experimental design; it is difficult for me as a reader to keep it all straight with only a textual description.

L158: change ”haphazardly” to ”arbitrarily”

L168-173: Is there any information on how a female may ”count” other females or eggs? Odors (e.g., L78-79)? Direct encounters? If LMC is sensed by females via odor, having 4 patches in the same box could essentially be sensed as a single patch by the females in that box. Have the authors considered this possibility, and how would that affect interpretation of results? Similarly, in the single 60-cm^2 patch per box, are the authors assuming that each mite somehow ”experiences” conditions across the full patch? Maybe odors can be sensed that far away, but if the cue requires contact (e.g. encounters with other mites or eggs), is it possible the patch is too big? This possibility is alluded to at the end of the paper, but not really discussed [L347-349]. Do the authors have information on how big a ”patch” in nature is?

L214: change to ”The sex ratio only of individual females could be obtained...”

L222-223: Is there support in the literature that can be cited for this method of determining significance? Requiring only > 5% of runs to have p<5% seems not very stringent for declaring signficance.

Table 1 is confusing. The caption for part A indicates that the values in the table are number of offspring per female; but the ”title” for part A in the table indicates the data are some sort of value for sex allocation. I think the authors are using the part A title to indicate their name for the experiments that these offspring number data came from, but this should not be done because of the confusion it can cause for the reader about what they are looking at in the table. When column headings differ, as they do for parts A and B of the table, this is an indication it needs to be split into two tables. In this case, it also means that the data in part B should be reported in the text, not in a table, because there is only one line of entries. Also, please include the p values in the table. L370: part of what is hard to keep straight is the use of ”females” for Gen. 1 and ”mothers” for Gen. 2. Could the authors say, ”and generation 2 when the grandmothers of the offspring were exposed to...” ?

The number of eggs laid by the females seems surprisingly low. I could be mistaken, but I thought T. urticae typically lay 100-200 eggs per female. If true, this suggests the mites are not being reared under optimal conditions; do the authors agree, and if so, how might this affect the results of their experiments and their interpretation?

Fig. 1: There are no A, B, or C panels labeled in the figure (although I can guess which they apply to).

L254-257: Relative to the baseline ratios in Generation 1 where level of LMC had no effect, the effect of maternal environment (gen 1) on sex ratio produced by the daughters (gen 2) was to increase the proportion of males at low LMC, not to increase the proportion of females at high LMC. So the wording of this sentence should be changed accordingly.

L265-266: In the Intro (L96-98), the authors cite Wrensch & Young 1975 and Roeder 1992 where females produced female-biased sex ratios under high LMC conditions. But this result was not seen in the current study where level of LMC had no effect (Fig 1A). What do the authors think may account for these conflicting results? I see the authors admit this in L290-291, but they do not address the reasons why their results differ, which should be examined.

L291-292: The number of females in the current patch may or may not provide reliable information (which would be independent of the population tested); all that can be said is that this population did not use that information as a cue under the conditions of the study.

L288: change ”for” to ”with”

L320-326: Rather than an alternative explanation, this seems the most likely (most parsimonious) explanation for the results, because it does not require cross-generational communication. The potential cue (juvenile crowding and/or frequency of encounters with siblings) is a direct experience of the individual female that will control sex allocation of her offspring.

L339-340: This is the right question, but only if the opposing results of previous studies on T. urticae (Wrensch & Young 1975; Roeder 1992) can be discounted in favor of the present study.

L347-349: The appropriate size of a patch is a serious question that the authors must consider in the experimental design, as I indicated above. It is related to the question of what form the actual cues take. It would seem important to discuss what is known about patch size and how that relates to the experimental design in the current study and perhaps in previous studies.

L349-350: It is not clear how "maternal cues [may] provide an integrative measure of population structure", nor how that would somehow be superior to knowledge of immediate conditions experienced directly by the female who is to make the sex allocation decision. I am not saying the authors are wrong, just that this argument needs to make the logic clearer so as to be more convincing.

## Reviewed by anonymous reviewer 2, 11 January 2018

Main comments: Hamilton (1967) predicted that, in a structured population, females would bias to produce more female offsprings to reduce Local Mate Competition (LMC) among sons and thus maximize her reproductive success. The spider mite (Tetranychus urticae) appears to be an ideal subject for experiments to test LMC as the species has a short turnaround generation time and the females can adjust the sex ratio of offsprings through manipulating the fertility rate of the eggs. The ability of adjusting offspring sex ratio seems to be heritable (i.e., females from the lines produce female-biased sex ratio usually produce more daughters than sons; Mitchell 1972), though it may be terminated if the females have experienced generations of high LMC (Macke et al. 2011). This Duncan et al. (2017) study further shows that, neither the kinship between the mating males and female, nor the presence/absence of other adult females in the same patch, but the LMC condition in the maternal environment was the cue influencing the daughters' offspring sex ratio.

The finding is interesting, although there are some drawbacks about the study. For instance, the observations were limited among two generations, and therefore it was unable to verify how many generations would be affected by the LMC cue experienced in a predecessor generation, and at what point the adjustment ability to be lost. The authors proposed some biological mechanisms to explain such maternal inference, but that does not sound very convincing: If the mothers can control the offspring sex ratio through manipulating the egg conditions in their daughters' ovaries, why can't they just adjust their own egg condition? Even if the living environment is indeed stable enough, what is the benefit to use maternal cues instead of immediate, social environment cues to adjust offspring sex ratio?

The result is certainly novel and worth publishing; however, I would probably recommend it as a reading material only for a journal club specialising in T. urticae behaviour.

Other comments: 1. Need references for the statement "Other studies have shown that spider mites can respond to both maternal cues and those in the immediate environment." (Line 94-96). 2. Check the citation for the statement "This study uses the same base population as Macke et al. 2011" (Line 123). There are two Macke et al. 2011 papers in the reference list. 3. How was the genetic relativeness in the 200 adult females in the new base population? (in Material and Methods) 4. There is no A, B, C marked in the Figure.

References: Hamilton, W. D. (1967). Extraordinary sex ratios. Science, 156(3774), 477-488. Macke, E., Magalhães, S., Bach, F., & Olivieri, I. (2011). Experimental evolution of reduced sex ratio adjustment under local mate competition. Science, 334(6059), 1127-1129. Mitchell, R. (1972). The sex ratio of the spider mite Tetranychus urticae. Entomologia experimentalis et applicata, 15(3), 299-304.