

University of Groningen

Sex determination meltdown upon biological control introduction of the parasitoid *Cotesia rubecula*?

de Boer, Jetske G.; Kuijper, Bram; Heimpel, George E.; Beukeboom, Leo W.

Published in:
Evolutionary Applications

DOI:
[10.1111/j.1752-4571.2012.00270.x](https://doi.org/10.1111/j.1752-4571.2012.00270.x)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2012

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

de Boer, J. G., Kuijper, B., Heimpel, G. E., & Beukeboom, L. W. (2012). Sex determination meltdown upon biological control introduction of the parasitoid *Cotesia rubecula*? *Evolutionary Applications*, 5(5), 444-454. <https://doi.org/10.1111/j.1752-4571.2012.00270.x>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

1 **Appendix I: Simulation model and likelihood functions**

2

3 Simulation model: The simulation was initiated by generating eight diploid virgin females with
4 n_{loci} unlinked CSD loci that are all heterozygous. Each virgin female produced a single haploid
5 genome through meiosis to obtain a son for the mother-son mating. Subsequently, diploid
6 offspring were produced by combining the son's genome and one of both maternal genome
7 copies (randomly sampled for each offspring). As in the experiment, all diploid offspring
8 produced by a mother were sired by the same son. Diploid males are produced if both genome
9 copies in a newly produced diploid offspring are identical. Diploid male survival, s , was
10 implemented by comparing a random number, drawn from a uniform distribution, against s . We
11 continued to generate adult diploid offspring from a single replicate until we matched the number
12 of diploid offspring that was produced for a particular replicate in the actual experiment. Hence,
13 while diploid family size was equal to the observed values, the number of surviving diploid
14 males varied according to n_{loci} and s .

15 For each mother in the mother-son generation, we then generated the same number of brother-
16 sister matings as in the experiment, unless a mother had produced only diploid sons, which is a
17 realistic consequence of the stochasticity resulting from CSD-allele segregation with a limited
18 number of CSD loci. In that case, no brother-sister matings were performed for that particular
19 mother. This happened only rarely in our simulations: in the most likely case of having 100%
20 male broods ($n_{\text{loci}}=1, s=1$), this occurred in 386 simulations out of 50,000 (0.72% of all
21 replicates). Brother-sister matings were generated by randomly sampling a daughter from the
22 mother's female offspring, and by generating a haploid son from that same mother. Again, a
23 mated daughter produced the same number of adult diploid offspring as in the actual experiment.

24 Likelihood functions: We denoted the proportion of diploid males x produced by a particular
25 mother k by x_k . We ran 50,000 replicate simulations of the inbreeding experiment, resulting in
26 50,000 simulated deviates of each data point, \hat{x}_k , for each set of model parameters $\mathbf{v} = \{n_{\text{loci}}, s\}$.
27 From a histogram of these simulated deviates \hat{x}_k , we obtained a simulated density function
28 $f_k(x_k|\mathbf{v})$ that informs us of the probability of the actual datapoint x_k given the current parameters.
29 For each data point x_k , the density function f_k was obtained from the frequency histogram of the
30 simulated deviates, which was smoothed using R's `approxfun()` method (R version 2.12.1,
31 R Development Core Team 2011). Figure S1 shows an example of the density function f_k . The
32 function is discrete since a female's fecundity values can only consist of integers, but nonetheless
33 provides us with a likelihood value that reflects the simulated outcome. Hence, the likelihood
34 function for an individual datapoint x_k is $f_k(x_k|\mathbf{v})$, and the total likelihood for the vector \mathbf{x} of all
35 datapoints resulting from the experiment is $L(\mathbf{x} | \mathbf{v}_i) = \prod_k^m f_k(x_k | \mathbf{v}_i)$. The overall likelihood
36 (taking logs and summing) is shown in Figure S2, the values of $L(\mathbf{x} | \mathbf{v})$ are shown for varying s
37 and $n_{\text{loci}} = \{1; 2; 3\}$.

38 Comparisons between different models were carried out with likelihood-ratio tests (LRTs). LRTs
39 are conventionally used to compare nested models (i.e., situations where one of the models is a
40 special version of the other, having additional parameters), with the null hypothesis that the data
41 are drawn from the simpler of the two models. However, LRTs can also be applied to models
42 that are non-nested (i.e., where one model does not have additional parameters compared to the
43 other), as is the case in our study. To do this, we used the following approach (for details see
44 Lewis et al. 2011): First, when comparing two non-nested models (say, model A and model B),
45 one cannot simply assign one of both models as a null model (unless prior information is
46 available). Instead, two reciprocal model comparisons are necessary, so that both models A and

47 B are considered as a null model. The observed value of the likelihood ratio test statistic $L(\mathbf{x}|\mathbf{v}_1)/$
48 $L(\mathbf{x}|\mathbf{v}_0)$ (see main text) falls into one of the following categories:

- 49 1. An LRT with A as the null model is non-significant, but an LRT with model B is
50 significant. Model A is therefore preferred over model B.
- 51 2. An LRT with B as the null model is non-significant, but an LRT with model A is
52 significant. Model B is therefore preferred over model A.
- 53 3. Both LRTs (A as a null model, B as a null model) are significant: neither model can be
54 considered appropriate.
- 55 4. Neither of the LRTs (A as a null model, B as a null model) are significant: no
56 discrimination between the models is possible.

57 In case of a comparison between non-nested models, significance of the likelihood ratio test
58 statistic cannot be calculated from the chi-squared distribution. Instead, we generated the
59 appropriate test distribution from the simulations of the experiment, assuming that the null
60 hypothesis is true. To generate the test distribution for a null hypothesis (which assumes the
61 particular parameter values \mathbf{v}_0), a set of 5,000 replicates was randomly sampled from the full set
62 of 50,000 replicate simulations for the parameter combination \mathbf{v}_0 . Every single datapoint, \tilde{x}_k ,
63 within each of these sampled replicates is now used as a datapoint to calculate a likelihood ratio
64 using the density function mentioned above, above, i.e.

65 $\tilde{L}(\tilde{x}_k | \mathbf{v}_1) / \tilde{L}(\tilde{x}_k | \mathbf{v}_0) = \sum_k^m (\ln f_k(\tilde{x}_k | \mathbf{v}_1) - \ln f_k(\tilde{x}_k | \mathbf{v}_0))$. This step was repeated for all 5,000
66 sampled simulations, resulting in a distribution of 5,000 likelihood ratio test values that were
67 then used for null hypothesis testing, summarized in Table 3. An example of a distribution
68 $q(\tilde{L}(\tilde{x}_k | \mathbf{v}_1) / \tilde{L}(\tilde{x}_k | \mathbf{v}_0))$ of likelihood ratio test values, in comparison to the actual likelihood
69 ratio is given in Figure S3.

70 Although significance values are not corrected for multiple comparisons, a Bonferroni correction
71 by multiplying significance values by $1/n=1/6$ does not alter our conclusions.