

LETTER TO THE EDITOR

A slow-growth high-mortality meta-analysis for insects: A comment on Chen and Chen

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Dear Editor,

Insect Science recently published a meta-analysis that tried to test support for the slow-growth high-mortality (hereafter SG-HM) hypothesis (Chen & Chen, 2018). Meta-analysis is a powerful statistical tool used to quantitatively compare and summarize multiple studies (Arnqvist & Wooster, 1995). However, results from a meta-analysis must be carefully interpreted when only limited sample sizes are available. Many conclusions made by Chen and Chen (2018) are based on low sample sizes and/or have small fail-safe numbers, which is problematic when making conclusions about whether the SG-HM hypothesis is supported or rejected.

The SG-HM hypothesis is based on the idea that development time of an herbivorous insect impacts its survival and thus also its fitness. The longer an insect feeds on a plant, the longer it is exposed to natural enemies (i.e., predators, parasitoids, and pathogens) or adverse climatic events, which increases its risk of mortality. Feeny (1976) first proposed that herbivores take more time to develop when they feed on low-quality plants (e.g., high chemical/physical defenses or low nutritional quality) than when they feed on high-quality plants, which presumably reduces herbivore fitness. Later, Price *et al.* (1980) predicted that the longer an herbivore in a vulnerable immature stage takes to develop into a reproductive adult, the greater the risk of attack by natural enemies; if an immature insect dies before reaching reproductive maturity, then fitness is reduced to zero. The SG-HM hypothesis has now been tested many times with studies both supporting or rejecting it for various reasons (e.g., Damman, 1987; Haggstrom & Larsson, 1995; Benrey & Denno, 1997; Fordyce & Shapiro, 2003; Lill & Marquis, 2001; Murphy, 2004; Medina *et al.*, 2005; Cornlissen & Stiling, 2006),

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and thus a comprehensive assessment of support for the SG-HM hypothesis in the literature would be valuable.

Chen and Chen (2018) performed a meta-analysis to test the conditions under which the SG-HM hypothesis is supported or rejected in herbivorous insect systems. This meta-analysis produced mean effect sizes for 52 different tests of the SG-HM hypothesis (e.g., comparisons among taxa, life stages, etc.). Of the 52 tests, 16 tests were significantly different from zero, which demonstrates support or rejection of the SG-HM hypothesis. All 16 significant tests were calculated with sample sizes of 20 or fewer effect sizes; 7 tests had sample sizes less than 10, and worryingly 4 tests had sample sizes of only 1 or 2. For example, the finding that SG-HM was rejected when studied in hymenopteran systems is based on a sample size of 1; this means that their conclusion regarding Hymenoptera is based on a single published study, and this result should not have been reported as a conclusion of a meta-analysis as it implies that the result has broad support. Similar caution should be applied to the conclusions about the effects of multiple parasitoid orders ($n = 2$), idiobiont parasitoids ($n = 2$), and predators alone impacting generalist herbivores ($n = 1$). Serious problems can arise in random-effects analyses performed with very low sample sizes, such as the analysis by Chen and Chen (2018), and it is critical that authors clearly explain limitations (Borenstein *et al.*, 2009). Additionally, it is important to consider nonsignificant results when sample sizes are low because the probability of type-II error is high, even though meta-analysis can be effective to avoid type-II errors with modest sample sizes. Of the 36 nonsignificant tests of SG-HM in the meta-analysis, 22 had sample sizes less than 10, and 11 had sample sizes less than 5. For example, the findings that studies measuring pupal mass or gall size neither supported nor rejected SG-HM were based on sample sizes that included only 2 effect sizes. We suggest that additional research and/or a more thorough review of the literature are needed to test these hypotheses.

Another meta-analysis issue is the file-drawer problem; results that contradict a favored hypothesis or that are nonsignificant tend to remain unpublished, and as such, languish in a file-drawer (Rosenthal, 1979). Thus, a meta-analysis may find a significant result because studies that support the tested hypothesis are disproportionately represented in the literature. To deal with this potential bias, researchers conducting a meta-analysis calculate a fail-safe number, which indicates the number of nonsignificant, unpublished papers that would need to exist to cause the significant effect that was found to become nonsignificant (Rosenberg, 2005). Fail-safe numbers that are large compared to the number of studies included in the test help assure us that the significant findings are not due to publication bias (Rosenberg, 2005). Chen and Chen (2018) report fail-safe numbers that are notably low. For example, 2 of the 16 significant tests have a fail-safe number of 0, which means that if even a single nonsignificant study were published, their effect size would be reduced to a nonsignificant value. Notably, for the 16 significant tests, 5 have fail-safe numbers of less than 10. Thus, for the significant results with low fail-safe numbers, there may be a file-drawer problem and the reported results may be due to a type I error.

The Chen and Chen (2018) review was timely given the number of times the SG-HM hypothesis has been tested in insect herbivore systems. However, because sample sizes were small and the risks associated with the file-drawer problem were not properly assessed, we should be cautious of drawing definitive conclusions about whether SG-HM is supported or refuted for the many subareas tested by Chen and Chen (2018). Readers unfamiliar with meta-analysis may overvalue conclusions made with small sample sizes or may fail to recognize the risks of the file-drawer problem. There may be other extenuating circumstances that should be considered as well. For example, one of the more reliable results that Chen and Chen (2018) appear to have found was that SG-HM was supported for generalist herbivores ($n = 16$, fail-safe number = 413), but not for specialist herbivores. However, Singer *et al.* (2012) suggested that only studies that experimentally control herbivore density can directly test SG-HM because many natural enemies (e.g., birds) forage for herbivorous prey (e.g., caterpillars) in a density-dependent way; since high-quality host plants often have greater densities of herbivores, these herbivores may suffer increased predation because they are found in high densities, which would mask any potential effects of SG-HM. Singer *et al.* (2012) found that if they controlled for herbivore density, then herbivores on poor-quality host plants were more likely to be depredated, supporting SG-HM; but if they did not control for density, then herbivores

on high-quality plants were more likely to be depredated, which does not support SG-HM (support instead for high-performance/high-mortality hypothesis). Without knowing how many of the papers reviewed by Chen and Chen (2018) controlled for herbivore density, it is difficult to know whether their findings are reliable. We argue that the real value of this review is that it highlights systems and questions where additional studies are needed to more fully test the SG-HM hypothesis.

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References

- Arnqvist, G. and Wooster, D. (1995) Meta-analysis: synthesizing research findings in ecology and evolution. *Trends in Ecology and Evolution*, 10, 236–240.
- Benrey, B. and Denno, R.F. (1997) The slow-growth-high-mortality hypothesis: a test using the cabbage butterfly. *Ecology*, 78, 987–999.
- Borenstein, M., Hedges, L.V., Higgins, J.P.T. and Rothstein, H.R. (2009) *Introduction to Meta-Analysis*. John Wiley & Sons, Ltd. The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, United Kingdom.
- Chen, K.W. and Chen, Y. (2018) Slow-growth high-mortality: A meta-analysis for insects. *Insect Science*, 25, 337–351.
- Cornlissen, T. and Stiling, P. (2006) Does low nutritional quality act as a plant defence? An experimental test of the slow-growth, high-mortality hypothesis. *Ecological Entomology*, 31, 32–40.
- Damman, H. (1987) Leaf quality and enemy avoidance by the larvae of a pyralid moth. *Ecology*, 68, 88–97.
- Feeny, P. (1976) Plant apparency and chemical defense. *Biochemical Interaction between Plants and Insects* (eds. J.W. Wallace & R.L. Mansell), pp. 1–40. Plenum Press, New York.
- Fordyce, J.A. and Shapiro, A.M. (2003) Another perspective on the slow-growth/high-mortality hypothesis: chilling effects on swallowtail larvae. *Ecology*, 84, 263–268.
- Haggstrom, H. and Larsson, S. (1995) Slow larval growth on a suboptimal willow results in high predation mortality in the leaf beetle *Galerucella lineola*. *Oecologia*, 104, 308–315.
- Lill, J.T. and Marquis, R.J. (2001) The effects of leaf quality on herbivore performance and attack from natural enemies. *Oecologia*, 126, 418–428.

- Medina, R.F., Barbosa, P. and Waddell, K. (2005) Parasitism levels in *Orgyia leucostigma* feeding on two tree species: implications for the slow-growth-high-mortality hypothesis. *Entomologia Experimentalis et Applicata*, 115, 193–197.
- Murphy, S.M. (2004) Enemy-free space maintains swallowtail butterfly host shift. *Proceedings of the National Academy of Sciences USA*, 101, 18048–18052.
- Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. and Weis, A.E. (1980) Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, 11, 41–65.
- Rosenberg, M.S. (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, 59, 464–468.
- Rosenthal, R. (1979) The “file drawer problem” and tolerance for null results. *Psychological Bulletin*, 86, 638–641.
- Singer, M.S., Farkas, T.E., Skorik, C.M. and Mooney, K.A. (2012) Tritrophic interactions at a community level: effects of host plant species quality on bird predation of caterpillars. *American Naturalist*, 179, 363–374.

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