

Misunderstood Mismatch

Michael C Singer¹ and Camille Parmesan^{1,2,3}

¹Station d'Écologie Théorique et Expérimentale, CNRS UMR 5321 and Université Paul Sabatier, 09200 Moulis, France ; ²School of Marine and Biological Sciences, University of Plymouth, Plymouth, PL4 8AA UK ; ³Department of Geological Sciences, University of Texas at Austin, Austin, Texas, 78712 U.S.A.

michael.singer@sete.cnrs.fr

camille.parmesan@sete.cnrs.fr

We need to understand and predict impacts of climate change on phenological synchrony between consumers and resources, since we are already seeing novel "mismatches" detrimental to consumers^{1,2}. To this end, Kharouba and Wolkovich³ (hereafter K&W) advocate developing approaches that combine theory and experiment to both forecast climate-change impacts and hindcast pre-climate-change "baseline" conditions. K&W provide a valuable review and cogent advocacy for future work, complementing their prior meta-analysis⁴ which showed that relative phenologies in interacting species-pairs are changing, but with no overall trend for increase or decrease of synchrony. However, K&W misinterpret examples from plant-insect interactions. Their detailed case study involves phenological synchrony/asynchrony between spring hatching of Winter Moth eggs and budburst of their oak hosts. The "novel" approaches they recommend for this system have mostly been done⁵⁻¹⁰, and a long-term baseline study of the role of variable asynchrony in Winter Moth population dynamics is ignored¹¹. Studies of insect/plant systems are misinterpreted by applying the well-established² definition of phenological synchrony as "the situation in which the most energetically demanding period of the consumer's life cycle overlaps with the period of peak resource availability." This definition worked well for the fisheries biologist¹² and ornithologists² who developed it, since parent birds require high caterpillar abundance when chicks are most demanding. However, it does not work for insects faced with the phenological task of fitting their life cycle into the time window when hosts are edible. For these species, the timing of peak host abundance is unimportant and the crucial phenological event often occurs when larvae are just hatched and least demanding of energy, not most demanding¹³. Here, we suggest a broader definition of synchrony that would work for most systems: "Phenological synchrony between consumer and resource occurs when the timing of their interaction maximizes the availability and/or the quality of the resource for the consumer." We also further document our data-driven conclusion¹³, subsequently modeled by others¹⁴⁻¹⁶, that asynchrony can be either adaptive or maladaptive for the consumer and that the baseline condition for our own study insect, the Bay Checkerspot butterfly, was adaptive asynchrony.

The Winter Moth/oak interaction has fascinated ecologists for decades, its complexity gradually emerging from a series of studies in different countries^{5-11,17-19}. Early egg-hatch before budburst can cause >90% mortality of neonate Winter Moth larvae from starvation¹¹, while synchronous hatch can result in total defoliation of oaks¹⁷. To test the assumption of the "Cushing hypothesis"¹² that phenological relationship with a resource controls consumer fitness, K&W use data from experiments conducted by Tikkanen & Julkunen-Tiitto¹⁰ to show that larval mortality of Winter Moth increased with deviation in both directions from synchrony, since larvae hatching before budburst risked starvation while late-hatching larvae died due to increasing host defenses. However, data on mortality alone are not the most appropriate to test the hypothesis. Eggs encounter a tradeoff between risk of mortality if they hatch early and reduced fecundity if they hatch late. The paper from which K&W extract their data on mortality¹⁰ also describes experiments that estimate fitness consequences of phenological synchrony from its combined effects on insect mortality and fecundity. This dataset, which is the appropriate one to use, shows a greater fitness penalty for early than for late hatch, tending to drive mean hatch time later than mean budburst (Figure 1).

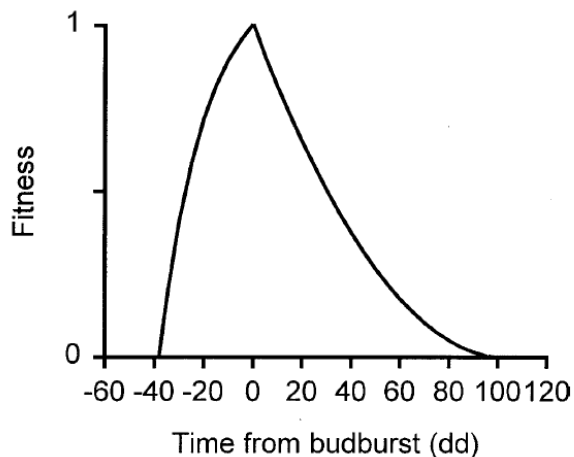


Figure 1: Combined effects of mortality and fecundity on Winter Moth fitness (y-axis) with differing deviations from synchrony between time of Winter Moth egg hatch and oak budburst (x-axis). X-axis scale is degree-days (dd) above 5°C. From Tikkanen & Julkunen-Tiitto¹⁰. Relationship derived from experimental manipulation of synchrony.

K&W suggest that novel understanding would come from combining the experiments on Winter Moth done by Tikkanen & Julkunen-Tiitto in Scotland¹⁰ with the field observations of van Asch & Vissers⁵ in the Netherlands. In the Dutch observations, the mean timing of egg hatch was asynchronous, always preceding oak budburst, but doing so to different extents in each year, indicating that moth and trees were using different cues to time spring development. K&W imply that this work was observational, hence minimally useful without being combined with the Scottish experiments. However, van Asch et al⁶ did include experimental assessments of the

effects of asynchrony on fitness, correctly combining the effects of phenology on fecundity and mortality. They also demonstrated heritability of egg hatch timing and predicted its evolution in response to climate change. The predicted evolution subsequently occurred⁷. Further, the Dutch group generated detailed analyses of climate effects on moth phenology⁸, while Buse & Good⁹ performed experiments in which both moths and oaks were subjected to simulated climate change. To a greater extent than K&W imply, the combination of observation and experiment that they recommend for the Winter Moth has been done.

K&W suggest that, in the absence of baseline information, hindcasting with "process-based models" could be used to deduce the baseline of the oak/Winter Moth system. Given current evolution of the moth's phenology⁷, hindcasting with ecological models is questionable. Further, baseline information does exist about the role of phenological asynchrony in the moth's population dynamics. From 1950-1966 Varley and Gradwell¹¹ measured the moth's population density each year, plus separate mortalities at different stages of the life cycle. They found that "winter disappearance," which they attributed almost exclusively to egg hatch before budburst, routinely caused more than 90% mortality of neonate larvae¹¹. Variation among years of this mortality factor was the main driver of year-to-year population changes (Figure 2).

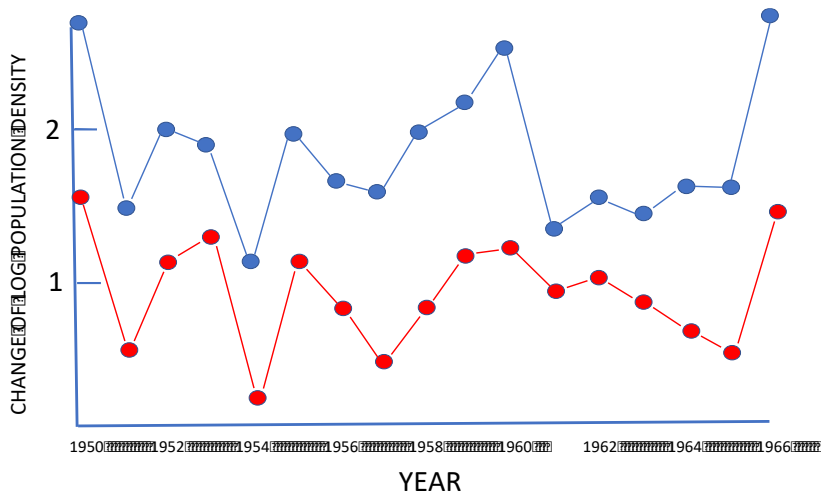


Figure 2. Varley & Gradwell's 17-year study¹¹ of the effect on Winter Moth population dynamics of variable asynchrony between egg-hatch and bud-burst. The upper line (blue) is population change between generations, calculated by subtracting log egg density in year $x-1$ from log egg density in year x ; the lower line (red) is the winter loss attributed to asynchrony, calculated by subtracting the log density of young feeding larvae in spring from that of eggs in the previous winter. The parallel nature of the graphs supports the authors' conclusion that variable asynchrony was the main driver of overall population dynamics.

Varley & Gradwell wrote¹¹: "Biologically, the amount of synchronization between egg hatch and bud burst determines the (population dynamic) changes." Apart from the assertion of a 4-5 day mean asynchrony between egg hatch and budburst¹⁸, this old study lacks detailed data on synchrony, concentrating instead on its effects on mortality. Nonetheless, it deserves to be

disinterred and reinstated into discussions of pre-climate-change baselines and the importance of consumer-resource phenological synchrony for population dynamics.

By applying their definition of synchrony to entomological studies, K&W misinterpret them. They define "asynchrony baseline" as "a hypothesis put forward by Singer & Parmesan¹³ that before climate change the most energetically demanding period of the consumer was not timed to the peak resource availability and thus consumer fitness was not at its maximum." This statement, which refers to work on a metapopulation of the Bay Checkerspot butterfly, is wrong in three respects. First, as in Winter Moth, mortality from asynchrony occurred in the least energy-demanding phase of the life cycle. Although eggs were laid on non-senescent annual hosts, most of those hosts died in the 2-3 weeks before the eggs hatched, causing mortality of neonate larvae that needed little food but found none at all. Second, the asynchrony baseline was not hypothesized but documented, resulting in mortality of 70-80% of neonate larvae in 1968, 1969 and 1970 and recorded again by other authors in 1983, 1984 and 1985¹³. Third, Singer & Parmesan¹³ argued that a fecundity-mortality tradeoff rendered this baseline asynchrony adaptive, not maladaptive (see below).

Adaptive asynchrony has multiple causes¹³⁻¹⁶. In the Bay Checkerspot it stems from intergenerational conflict. A female larva that has achieved the minimum size for pupation may continue to feed, thereby increasing both her own fecundity and her offspring's asynchrony with availability of edible hosts. Her interests and those of her larvae are in conflict, but she acts first and controls their fates. Field-gathered data on larval growth rate and temporal pattern of host senescence under baseline conditions generated the prediction that delaying adult eclosion by one week in the middle of the flight season in 1970 would have increased maternal fecundity by 200 - around 25% - while adding only 10% to offspring mortality from host senescence¹⁵. At this point natural selection acting on mothers was favouring prolonged development (later eclosion). The documented asynchrony of larvae with their hosts was adaptive for their mothers but maladaptive (a mismatch) for themselves.

Unlike the Winter Moth, in which precise synchrony of egg hatch with budburst can approximately maximize fitness for an individual trading its own fecundity against its **own** chances of survival, the adaptive strategy for a Bay Checkerspot female, both prior to climate change and during it, is to force her offspring into vulnerable asynchrony. From the beginning of the series of Bay Checkerspot studies, the density-independence and climate-dependence of asynchrony-caused mortality predicted unstable population dynamics¹⁸. Eventually, permanent extinction of the metapopulation in 1998 was attributed to climatic fluctuations associated with warming²⁰.

Some authors use "mismatch" and "asynchrony" as synonyms^{2,3}, while others restrict mismatch to maladaptive asynchrony^{15,21}. We hope that our account clarifies the restricted nature of the popular definitions of synchrony & mismatch adopted by K&W, suggests a more inclusive definition and brings informative old studies back into circulation.

REFERENCES

1. Renner, S. S., & Zohner, C. M. Climate Change and phenological mismatch in trophic interactions among plants, insects and vertebrates. *Annu. Rev. Ecol. Evol. S.* **49**, 165-182 (2018).
2. Visser, M. E. & Gienapp, P. Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* **3**, 879-885 (2019).
3. Kharouba, H. M. & Wolkovich, E. M. Disconnects between ecological theory and data in phenological mismatch research. *Nat. Clim.; Chang.* **10**, 406-415 (2020).
4. Kharouba, H. M., Ehrlen J., Gelman, A., & Wolkovich, E. M. Global shifts in the phenological synchrony of species interactions over recent decades. *Proc. Natl. Acad. Sci. USA* **115**, 5211-5216 (2018).
5. van Asch M. & Visser, M. E. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annu. Rev. Entomol.* **52**, 37-55 (2007).
6. van Asch, M., van Tienderen, P. H., Holleman, L. J. M. & Visser, M. E. Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Glob. Chang. Biol.* **13**, 1596-1604 (2007).
7. van Asch, M., Salis, L., Holleman, L. J. M., van Lith, B. & Visser, M.E. Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nat. Clim. Chang.* **3**, 244-248 (2013).
8. Salis, L., Lof, M., van Asch, M. & Visser, M. E. Modeling Winter Moth *Operophtera brumata* egg phenology: nonlinear effects of temperature and developmental stage on developmental rate. *Oikos* **125**, 1772-1781 (2016).

9. Buse, A. & Good J. E. G. Synchronization of larval emergence in winter moth (*Operophtera brumata*) and budburst in pedunculate oak (*Quercus robur*) under simulated climate change. *Ecol. Entomol.* **21**, 335-343 (1996).
10. Tikkanen, O-P & Julkunen-Tiitto, R. Phenological variation as protection against defoliating insects: the case of *Quercus robur* and *Operophtera brumata*. *Oecologia* **136**, 244-251 (2003).
11. Varley, G. C. & Gradwell, G. R. Population models for the winter moth. In: *Insect Abundance, Symp. Roy. Ent. Soc. Lond. No. 4*, ed. Southwood, T. R. E., pp 132-142 (1968).
12. Cushing, D. H. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* **26**, 249-293 (1990).
13. Singer M. C. & Parmesan, C. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Phil Trans R Soc B* **365**, 3161-3176 (2010).
14. Johanson, J. & Jonzen, N. Game theory sheds new light on ecological responses to current climate change when phenology is historically mismatched. *Ecol. Lett.* **15**, 881-888 (2012).
15. Johansson, J., Kristensen N. P., Nilsson, J-Å. & Jonzén N. The eco-evolutionary consequences of interspecific phenological asynchrony - a theoretical perspective. *Oikos* **124**, 102-112 (2015).
16. Visser, M. E., te Marvelde, L., & Lof, M. E. Adaptive phenological mismatches of birds and their food in a warming world. *J. Ornithol.* **153** (suppl), S75-S84 (2012).
17. Feeny, P. Seasonal changes on oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* **51**, 565-581 (1970).

18. Wint, W. The role of alternative host plant species in the life of a polyphagous moth, *Operophtera brumata*. *J. Anim. Ecol.* **52**, 439-450 (1983)
19. Holliday, N. Population ecology of winter moth (*Opheoptera brumata*) on apple in relation to larval dispersal and time of bud burst. *J. Appl. Ecol.* **14**, 803-813 (1977).
20. McLaughlin, J. F., Hellmann, J. J., Boggs, C. L. & Ehrlich, P. R. Climate change hastens population extinctions. *Proc. Nat. Acad. Sci. USA* **99**, 6070-6074 (2002).
21. Samplonius, J. M., Atkinson, A., Hassall, C..... Phillimore, A. B. Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts. (2020) Preprint: <https://ecoevorxiv.org/jmy67>