Misunderstood Mismatch

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We need to hone our ability to predict impacts of climate change on phenological synchrony between consumers and resources, since we are already seeing novel "mismatches" detrimental to consumers1-3. To this end, Kharouba and Wolkovich4 (hereafter K&W) advocate combining theory and experiment to both forecast climate-change impacts and hindcast pre-climate-change "baseline" conditions. We question the feasibility of hindcasting, but show that more detailed baseline information exists than K&W describe. In their case study of synchrony/asynchrony between Winter Moths and their oak hosts, K&W omit a baseline study done from 1950-19665 and underestimate the extent to which the approaches they recommend have already been done6-11. They define "phenological synchrony" as "complete overlap between the most energetically demanding period of the consumer and the peak of resource availability." This leads them to define "asynchrony baseline" as "a hypothesis 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 maximum." K&W's reference for this definition is a study of Edith's Checkerspot butterfly12 providing baseline (1968-71) data illustrating that asynchrony was adaptive, not maladaptive: the opposite of K&W's assertion. Further, while peak resource timing is important to birds(1,2) it is not relevant to insects tasked with fitting their life cycles into time windows when hosts are edible. For many insects, including both Winter Moth and Checkerspots, high mortality caused by asynchrony occurs when larvae are newly-hatched and least demanding of energy12, not most demanding. Application of K&W's definition of asynchrony to these systems engenders misunderstanding. Here, we suggest a definition of synchrony that could work for birds and insects: "phenological synchrony between consumer and resource occurs when the timing of their interaction allows the consumer to benefit fully from the availability and/or the quality of the resource."

K&W complement their valuable meta-analysis on observed changes of phenogical synchrony in species-interactions3 by providing cogent advocacy for future work4. However, their case study for this advocacy, the Winter Moth/oak interaction, is misunderstood. This interaction has fascinated ecologists for decades, its complexity gradually emerging from a series of studies in different countries5-11,13-15. Early egg-hatch before budburst can cause >90% mortality of neonate Winter Moth larvae from starvation5, while synchronous hatch can result in total defoliation of oaks13. To test the assumption of the "Cushing hypothesis" that phenological relationship with a resource controls consumer fitness, K&W use data from experiments conducted by Tikkanen & Julkunen-Tiitto11 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 mortality11 also describes experiments that estimate fitness consequences of phenological synchrony from its combined effects on insect mortality and fecundity. This dataset, which is the more 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).

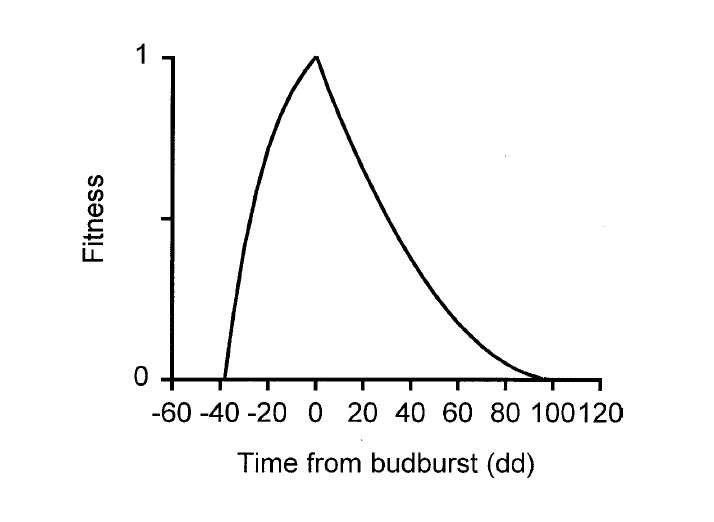


Figure 1: Combined effects of mortality and fecundity on Winter Moth fitness (y-axis) with differing deviations from sychrony between time of Winter Moth egg hatch and oak budburst (x-axis). X-axis scale is degree-days (dd) above 5°C. FromTikkanen & Julkunen-Tiitto11. Relationship derived from experimental manipulation of synchrony.

K&W suggest that novel understanding would come from combining the experiments on Winter Moth done by Tikkanen & Julkunen-Tiitto in Scotland11 with the field observations of van Asch & Visser6 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 al7 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 occurred8. Further, the Dutch group has generated detailed analyses of climate effects on moth phenology9,while Buse & Good10 performed experiments in which changes in synchrony were measaured when both moths and oak saplings 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. Much progress has been made in using these sophisticated eco-evolutionary models to forecast combinations of plastic and evolutionary responses to environmental variation16. However, they have not been used for hindcasting, which is inherently more difficult, especially when phenological traits are known to be currently evolving, as they are in the Winter Moth. However, long-buried baseline information does exist about the role of phenological asynchrony in the Winter Moth's population dynamics. From 1950-1966 Varley and Gradwell5 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 larvae5. Variation among years of this mortality was determined by Varley & Gradwell to be the "key factor" in the moth's population dynamics; i.e., the main driver of year-to-year population changes (Figure 2).



Figure 2. Varley & Gradwell's 17-year study5 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 wrote5: "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 budburst14, 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.

Following common usage among phenologists2, K&W define "phenological synchrony" as "complete overlap between the most energetically demanding period of the consumer and the peak of resource availability." This usage leads them to define "asynchrony baseline" in their glossary as "a hypothesis put forward by Singer & Parmesan 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." However, the reference that K&W give for this definition12 is a study of Edith's Checkerspot butterfly providing baseline data documenting a fecundity-mortality tradeoff that rendered this baseline asynchrony adaptive, not maladaptive. Further, checkerspot mortality from asynchrony occurred in the least energy-demanding phase of the life cycle, not the most demanding period as required by the definition. 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.

Adaptive asynchrony has multiple causes17-19. In the Bay Checkerspot it stems from intergenerational conflict12. 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 the already high offspring mortality from host senescence12. At this point natural selection acting on mothers was favouring prolonged development and later eclosion.

The asynchrony of checkerspot larvae with their hosts resulted in neonate mortality of 70-80% in 1968, 1969 and 1970 and was recorded again by other authors in 1983, 1984 and 198512. 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 survival6-11, 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 dynamics12. Eventually, permanent extinction of the metapopulation in 1998 was attributed to climatic fluctuations associated with warming20.

Some authors use "mismatch" and "asynchrony" as synonyms2,3, while others restrict mismatch to maladaptive asynchrony17,21. Independently of this discussion, we lack definitions that would apply to species like the checkerspots and Winter Moths, that suffer phenological stress from being constrained to fit their life cycles into short time windows. Hence, we suggest a broader definition of synchrony than that adopted by K&W: "phenological synchrony between consumer and resource occurs when the timing of their interaction allows the consumer to benefit fully from the availability and/or the quality of the resource."

We hope that our account clarifies the evidence for adaptive baseline asynchrony, reveals the restricted nature of popular definitions of synchrony & mismatch, suggests a more inclusive definition and brings informative old studies back into circulation.

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