Misunderstood Mismatch

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It is not controversial that 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 Wolkovich[3] (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. However, they misunderstand and 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 that K&W recommend for this system have mostly been done, and a long-term baseline study of the role of variable asynchrony in Winter Moth population dynamics is ignored. Published studies of insect/plant systems are misinterpreted by applying a 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 resource availability." This definition works well for ornithologists, since parent birds require high caterpillar abundance when chicks are most demanding. However, the important role of phenological synchrony in most insect-plant systems is to fit the insect life cycle into the available time, and the crucial phenological event often occurs when larvae are just hatched and least demanding of energy, not most demanding.

The Winter Moth/oak interaction has fascinated ecologists for decades, its complexity gradually emerging from a series of studies in different countries[4-12]. Early egg-hatch before budburst can cause >90% mortality of neonate Winter Moth larvae[4] from starvation, while synchronous hatch can result in total defoliation of oaks[5]. To test the assumption of the "Cushing hypothesis"[13] that phenological relationship with a resource controls consumer fitness, K&W use data from Tikkanen & Julkunen-Tiitto[8] 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 encountered increasing host defenses. However, data on mortality alone are not the most appropriate to test the hypothesis. Ever since Feeny's[5] experiments in which he fed Winter Moth larvae oak leaves of differing age, it has been clear that the principal penalty for late egg hatch is reduced fecundity. 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 mortality[8] 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, predicts evolution of slight asynchrony, with mean hatch time later than mean budburst (Figure 1).

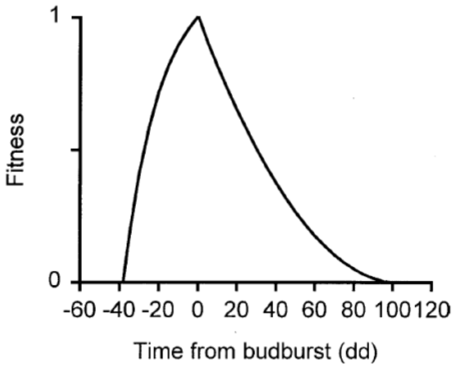

Figure 1: Combined effects of mortality and fecundity on Winter Moth fitness (y-axis) with differing deviations from sychrony between time of Winter Moth egg hatch and oak budburst (x-axis). X-axis scale is degree-days (dd) above 5°C. From Tikkanen & Julkunen-Tiitto 2003.'

K&W suggest that novel understanding would come from combining the experiments on Winter Moth done by Tikkanen & Julkunen-Tiitto in Scotland[8] with the field observations of van Asch & Visser[9] in the Netherlands. In these 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 al[10] 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 occurred[11]. Further, the Dutch group generated detailed analyses of climate effects on moth phenology[12] while Buse & Good[7] 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 already been done.

K&W suggest that, in the absence of baseline information, hindcasting with "process-based models" could be used deduce the baseline of the oak/Winter Moth system. Given current evolution of the moth's phenology[11], 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 Gradwell[4] 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 larvae[4]. Variation among years of this mortality factor was the main driver of year-to-year population changes (Figure 2).

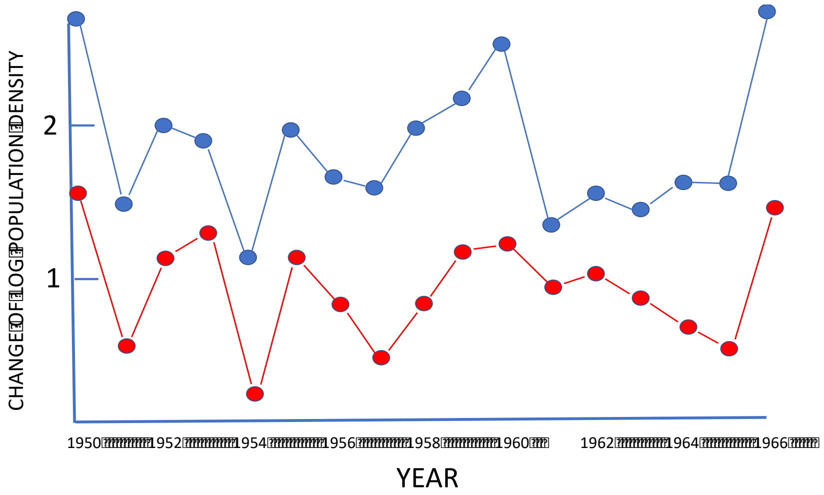

Figure 2. Varley & Gradwell's (1968) 17-year study of the effect on Winter Moth population dynamics of variable asynchrony between egg-hatch and bud-burst. The upper line (blue) is population change between generations, calculated by subtracting log egg density in year x-1 from log egg density in year 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 wrote: "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 budburst[14], 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 & Parmesan[15] 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 immediate mortality of neonate larvae that needed little food but found none at all; they were simply unable to fit their life cycles into the available time window. Second, the asynchrony baseline was not hypothesized, it was documented, resulting in mortality of an estimated 70-80% of neonate larvae in 1968, 1969 and 1970 and recorded again by other authors in 1983, 1984 and 1985[15]. Third, as we detail below, a fecundity-mortality tradeoff rendered this baseline asynchrony adaptive, not maladaptive as K&W state.

Adaptive asynchrony has multiple causes[15,16,17]. In the Bay Checkerspot it stems from choices made by female larvae to continue to feed after they have grown large enough to pupate, thereby increasing both their own fecundities and the asynchronies of their offspring with hosts. 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 within the flight season would increase maternal fecundity by around 25% while adding only 10% to offspring mortality from host senescence[15]. Thus, prior to climate change, natural selection favored asynchrony. K&Ws assertion that baseline asynchrony showed that "consumer fitness was not at its maximum" is wrong. In fact, baseline data from the checkerspot fit K&W's definition of "adaptive mismatch." 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 chances of survival, the adaptive strategy for a Bay Checkerspot female 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 mortality caused by asynchrony predicted instability of population density[15]. Eventually, permanent extinction of the metapopulation in 1998 was attributed to climatic fluctuations associated with warming[18].

We hope that this account clarifies an important difficulty with the current definition of phenological synchrony and brings back into circulation old studies that are informative, despite failure to meet criteria for inclusion into modern meta-analyses.

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