PHENOLOGICAL HISTORIES

From listening to Varley in 1963 I had expected to find old data showing that that the baseline for the Winter Moth/oak system was clearly asynchrony, but in fact all that I found was a pers. comm from Gradwell reported by Wint (1983) that the mean baseline asynchrony was 4-5 days before budburst. Gradwell was a cautious, understated fellow, so he was probably correct, but it's anecdotal. In contrast, the dataset that I remember Varley discussing in detail, relating year-to-year changes in synchrony to population dynamics is useful and should resurface (Varley & Gradwell 1968). I've re-drawn their graph below. The upper line is the population change between generations, calculated by subtracting log egg density in year x-1 from log egg density in year x; the lower line is the winter loss attributed to asynchrony, calculated by subtracting the log density of young feeding larvae in spring from that of eggs in winter. The parallel nature of the graphs supports V&G's conclusion that variable synchrony among years was the main driver of overall population dynamics.



Very soon after listening to Varley and Feeny I found myself also working on a plant-insect system, the Bay Checkerspot, that showed repeated strong asynchrony. I followed the fates of naturally-laid egg clutches and estimated 70-80% mortality of neonates in each of four years (1968-71). Most eggs hatched after hosts had senesced and larvae starved without eating anything at all. I have sad Ektachrome slides of tiny larvae looking for nonexistent food. This mortality was followed by another 80% or so caused by the same asynchrony, because even among larvae that did find food as neonates, most were killed by host senescence before they had fed for the 2-3 weeks necessary to reach diapause. The reason for this routine asynchrony was that mothers can dramatically increase their fecundity by extending larval feeding, but this delays their eclosion as adults and subsequent oviposition.

In 1970 I measured the temporal pattern of host senescence by censusing each week the environs of the same 290 randomly-chosen points in a large habitat patch with diverse aspects of slope. In our 2010 Phil Trans paper we put these censuses together with larval growth rates in the field and showed that, if, in mid-flight season, a female delayed emergence for a week, she could increase her fecundity by around 25% and would increase offspring mortality by less than that, around 10%. So response to natural selection on maternal fecundity was responsible for driving their offspring into a strong asynchrony that was lethal for the majority. In the 2010 paper we argued that this was an adaptive baseline asynchrony that caused density-independent mortality and population instability. Two sets of researchers confirmed the same asychrony in 1983,1984 and 1985 and it eventually contributed to to climate-change-assisted extinction of the long-studied metapopulation in 1998 (McLaughlin et al 2002 PNAS).

Our espousal of adaptive asynchrony was picked up by Johannson & Jonzen (2012 Ecol Lett) who cited us copiously and correctly and began their paper with this quote from our paper: "to the extent that species' interactions might have had an evolved asynchrony or mismatch as their starting point, assumptions of baseline synchrony would risk mis-detection, mis-estimating and mis-attribution of climate change impacts." We thought: "Great, we've made our point!" However, in contrast to Johansson, Marcel, whom we had consulted at length while writing our Phil Trans piece (and because Camille was Margriet van Asch's external examiner) seems to have been unhappy that we had come up with a novel idea in HIS field, so he decided to bury it. His 2012 paper titled "Adaptive phenological mismatches..." doesn't cite our 2010 paper that both introduced the topic and gave a worked example in the form of the checkerspot study.

So, you'll appreciate, I hope, that it's frustrating to see his paper cited in your glossary as the source of the "adaptive mismatch hypothesis." It's also frustrating to see you define "asynchrony baseline" 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." This statement is triply wrong. First, as in Winter Moth, mortality from asynchrony occurred in the least energy-demanding phase of the Checkerspot life cycle (in our MS, we argue that your definition of synchrony does not apply to most plant-insect systems). Second, the asynchrony baseline was not hypothesized, it was documented, I spent many cold March and April days censusing plants around my 290 random points and following the fates of natural egg clutches. Third, although we did not calculate a precise value for optimal timing, we did show that any adaptive strategy would involve considerable baseline asynchrony. We did not colclude that "consumer fitness waas not at its maximum," quite ther contrary.

I really enjoyed your 2018 PNAS paper and think it a valuable advance. However, it contains a fourth, competely different, misunderstanding of our checkerspot work. You write" In systems where asynchrony may be the baseline...(Singer & Parmesan 2010) climate-change driven shifts in synchrony may not lead to substantial effects in fitness." This is the opposite of our argument. By evolving adaptively to the outer limits of their climatic tolerance the butterflies render themselves even more susceptible to climate-caused shifts in synchrony than they would have been with a synchrony baseline. These shifts could have very positive or very negative effects. No surprise that climate-change-induced increasing asynchrony (driven by increasing variability of rainfall) was later blamed by McLaughlin et al (2002) for the extinction in 1998 of the small metapopulation that I had studied in the 1960's and where Ehrlich and his students had worked since the 1950's.

Adaptive evolution increased climate-sensitivity of our butterflies in multiple ways; I think that the clearest summary I've made for these processes is in the Figure caption to the PNAS commentary that I attached along with this autobiography. I sent this PNAS piece to Suzanne Renner as she was writing her review, requesting that she include our work on adaptive mismatch and, if she wished for a quick and simple explanation, to check the Figure caption. But it seems that I didn't get through to her at all.

Our 2010 paper is well-cited, but, with the exception of Johanssen, it has been consistently misinterpreted, most usually cited as evidence that current asynchrony IS evidence for climate change impacts, rather than as a cautionary tale against such interpretation as we had intended. In retrospect, we shouldn't have titled it with a question. I gave a talk at the Evolution meetings about evolution to the limits of ecological tolerance and a TREE editor in the audience invited me to submit a MS on that topic, so that is the avenue through which I'll expand the argument that began in my PNAS commentary.

Finally, and independently of our response to your paper, I'd like to inform you of our current interests in the interactions between adaptive asynchrony and diet evolution in our checkerspots. We have published three case histories. In one case, the spatial pattern in a geographic mosaic of plant-insect interaction across a few hundred km was driven by the degree of phenological synchrony with a short-lived annual host that was poorly-defended chemically. At sites where this host's lifespan was shortest the asychrony with it would have been most extreme, if it had been used.. but it was not; the insects and had evolved adaptation to a well-defended plant that was longer-lived and with which they had complete synchrony. At sites where asynchrony with the annual was less (but still asynchronous), the butterflies were highly adapted to it and monophagous on it (Singer & McBride 2012 Ecology). In the second case, adaptive asynchrony with a short-lived annual set the stage for butterflies to raise fitness by colonizing an exotic perennial to which they were not adapted but also not asynchronous. The result was evolution into a lethal eco-evolutionary trap and population extinction (Singer & Parmesan 2018 *Nature*). In the third case, human activities (logging) reduced the degree of asynchrony with a poorly-defended host that was not used, causing insects to evolve preference for it and adopt it as their principal host. Using this novel host raised fitness despite a suite of six maladaptations to it. However, succession across four decades gradually regenerated the asynchrony until the insects were forced back to their original diet (Singer & Parmesan 2019 Evol Appl.)