-coevolution arms race- and interaction with phenological cues

DEFINING MISMATCH

* Options:
  + Operational definition- i.e. not defined by fitness
    - Time-based
    - Relative timing=consumer phenology- resource phenology
    - Match=zero difference in days
  + Functional definition- highest fitness at 0 mismatch/MATCH (Cushing)
    - Match= fitness is highest when most energetically expensive part of consumer’s phenology=peak food availability
    - Mismatch= decrease in fitness when gap between food requirement and availability; when food requirement is mistimed relative to peak availability of food resources
    - Cushing observed that the mean timing of peak fish spawning was fixed from year to year, whereas the appearance of zooplankton populations was regulated from the bottom-up by stochastic climatic processes. Therefore, consumers will be less likely to track variability in resource phenology which has disproportionately larger consequences on population recruitment than other life history stages
  + Baseline- **experiments- \*\*count how many use baseline to judge match, has to be a priori**
    - Studies assuming baseline=maximum fitness
    - Singer and parmesan predict much weaker relationship and/or much higher inter-annual variation BECAUSE resource phenology not key factor driving consumer fitness
* Can use cues to predict mismatch in year X before climate change, how to get Y fitness? Can inform model with theoretical limit (e.g. caterpillar emerges in Feb) to inform curve but would have huge confidence intervals! Need process based models with fitness. Extrapolation!
* Ideally want to measure most energetically expensive part of consumer’s phenology BUT in many cases use phenological phase proxy instead of actual key event (e.g. use lay date for chick activity) either because it’s not known or not specified
* ~~Trait-mediated effects- altering phenotypes (usually behavioural, morphological and/or physiological plasticity) in response to abiotic and biotic pressu~~res
* Aquatic vs. terrestrial
  + Food web dynamics- top down in aquatic systems, no consumer impact on resource population dynamics (terrestrial- won’t affect tree population dynamics), terrestrial- different generation times between consumer and resource, vs. aquatic- more similar generation times
  + Rescale mismatch by generation time? Body size?
    - How many generations of phyto or zooplankton per season?
  + Should impacts be stronger in aquatic because stronger trophic cascade theory/food web theory?
  + Should impacts be stronger in terrestrial because every generation is re-set whereas in aquatic multiple generations occur without being “reset” by abiotic factors
  + Aquatic- top down (consumer before resource)
  + Terrestrial- bottom up
  + No specialization in aquatic
  + Defenses for resources in aquatic- next generation of daphnia (zooplankton) will have helmets, make it harder for gape feeders because they are now bigger- maternal effect, not genetic change; phytoplankton- how much silica, makes it less nutritious ~ chemical
  + The way phenology is measured is different- e.g. phytoplankon’s phenological events are based on population-level processes and not individual life-history events (e.g. timing of peak population size which represents a balance of reproduction and mortality/loss)
  + Cue differences between aquatic vs terrestrial
    - Aquatic- cues are only important for first generation, all other generations based on density dynamics (1) abiotic cue for phytoplankton to start the season, later generations- based on density dependence; (2) zooplanklton- what cues? Biotic?

FITNESS-MISMATCH RELATIONSHIP

* Mismatches are proposed to be strong drivers of population dynamics (Moller et al. 2008) BUT empirical evidence for mismatches leading to population declines is limited
* Shape of relationship- what is true relationship?
  + Hump-shaped- best fitness is at some match and decreases in both directions- tests “true” match
  + Linear- fitness decreases with increasing mismatch
  + How to figure out shape?
    - Experiments- Predefine mismatch based on baseline for experiments OR Thackeray et al. 2016 predictions- Schenk et al 2017
    - Observational- move towards predictive- need phenological cues of consumers and all resources to predict baseline match,
* Unequal fitness consequences- different fitness consequences depending on what part of curve (Singer and Parmesan)
* Optimal timing is a function of many different types of selection (e.g. depends on trade-offs between the costs of (a-)synchrony and the costs of mistiming other events)
* Need to specify where fitness is going to be 0 if you can’t do experiments
* Early consumer phenology relative to resource means different things for different interactions
  + Different resources used
  + Interaction type changes
  + Not measuring phenological phase of interest (🡺 include estimate of time lag)
  + Look at figure 26.1 in Kerby chapter- presented as consumer first!

STANDARDIZING MISMATCH

* Calculated as the difference in days between events that are most relevant to that interaction
* Magnitude: Ideally want larger values= greater mismatch= further days apart from resources= bad thing for consumers
  + Sometimes not clear (e.g. in HMK031, HMK036)
  + Breaks down in aquatic systems because quick turnaround between producers and consumers- temporal sequencing is difficult to determine therefore sampling frequency is important; AND- some zooplankton not in complete dormancy, some remain at low densities
  + OR further apart could be better (HMK041, HMK058)
    - E.g. Pyrenean chamois and spring vegetation- early onset of spring leads to increased access to food, so larger differences=better fitness BUT must be theoretical limit at some point
* Direction: Ideally want positive values (i.e. when food is available) =what’s better for consumers
  + But dependent on biology of system- it could take 5 days for adult butterfly to feed, mate, oviposit so, -5 is better than 0
* What is most favourable period? E.g. insects prefer young leaves whereas flower- and seed-eating weevils depend on flowering date or seed seeding period

EVALUATING CONSEQUENCES

* Assuming mismatch effects will be visible on X measure of fitness (but could be wrong measure), proxies could be crude index of actual success
* Assuming reproductive success is largely determined by synchrony (temporal overlap)
* (similar to above\_ assuming consumer reproduction/population growth is limited by resource availability during some of the year

FACTORS AFFECTING (short-term) CONSEQUENCES

* short-term= within-season dynamics- can account for processes such as emergence, competition and death for univoltine consumers
* Length of period over which food is available (width of food peak) and maximum amount of biomass available (height of peak) also important
  + Also changing
  + Good timing but not much food can be outweighed by poor timing but large amount of food (HMK003)
* Resource and/or consumer abundance can influence the strength of a trophic match/mismatch by changing likelihood that consumers will encounter resources at the tails of their temporal distributions
* Temporal variance- phase duration
* Evolutionary context
  + Selection pressures on flowering time just in terms of interactions- synchronizing reproduction with pollinators, minimizing overlap with florivores and competitors for floral resources, avoiding seed predators
* Life-history strategies
  + Capital (build up energy surplus throughout the year) vs. income (high costs of reproduction so need continuous influx of energy) breeders
* *More likely* to find consequences when:
  + Specialist feeders (high interaction strength)
  + [for generalists- will depend on ability/possibility of prey switching]
  + Highly seasonal environments-
    - Narrow windows for consumers
    - Narrow production pulses in resources (length of resource period depends on trade-offs faced by the resource, e.g. long emergence period could be a bet-hedging strategy to survive in an unpredictable environment)
  + Systems without high interannual variation
  + Either very early or very late-season species
* *Less likely* to find consequences when:
  + Stronger selection from abiotic conditions (direct effects; e.g. too cold, frost)
  + Strong intraspecific competition
  + Strong density dependence because overrun by environmental stochasticity more than phenology
  + Interannual variability in food quantity and environment
    - Bed-hedging strategy- longer phenological phase duration (Kerby chapter)
  + High food baseline levels
  + Turnover rates and prolonged seasonal availability allowing extended periods of production

FACTORS AFFECTING LONG-TERM CONSEQUENCES

* Long-term=multiyear, i.e. net success of a population from one year to the next, processes like birth, overwingtering
* Depends on importance of the interaction and the likelihood of a significant mismatch
  + Importance= degree to which the demography or population size of one species relies on the interaction occurring
  + Significant mismatch= probability that the interaction might fail ( at least functionally)
* Different process at individual vs. population level (e.g. balance between survival and reproduction, variation in phenological responses across population)
* Age-size structure of population (via density dependence)
* Resiliency- ability to overcome; how quickly can negative impact of mismatch be overcome in response to subsequent favourable conditions?
  + Generation time
* Life-history tradeoffs- mistiming with optimum food may not be so selectively disadvantageous if this means a lower predation risk (Singer and Parmesan)
* Relative importance of internannual variation in temporal overlap vs. long term direction change (miller-rushing et al. 2010)
* Baseline synchrony- are species adapted to be asynchronous
  + In antagonistic interactions- one of the partners is selected to be more mismatched- therefore more likely these interactions are likely to be mismatched in the first place
  + For mutualistic interactions- we expect both partners to be selected to maximize synchrony
* Effect of other resources
  + What is most important factor regulating the population?

Quick survey of experiments

HMK001- mismatch driven by temperature (aquatic)

HMK002- mismatch driven by temperature (aquatic)

HMK005- match defined by previous work in the system (terrestrial)

HMK014- mismatch driven by temperature (terrestrial)

HMK015- mismatch driven by temperature (terrestrial)

HMK017- mismatch driven by temperature (terrestrial)

HMK019- match defined by previous work in the system (Hmk020); mismatch chosen based on temperature thresholds (terrestrial)

HMK020- match defined by previous work in the system from 1992 and 1999; Hunter and Elkinton 2000- used natural observations of match from year of experiment (done in 1995 and 1996)

Schenk et al. 2017- uses Thackeray predictions to determine mismatch

Keywords:

Demography-population vital rates- reproduction and survival

Additional papers to read:

Dunn et al. 2011. Ecology- A test of the mismatch hypothesis: how is timing of reproduction related to food abundance

Dunn and Moller 2014. Changes in breeding phenology and population size in birds.

Hipfner, J. M. (2008) Matches and mismatches:

ocean climate, prey phenology and breeding

success in a zooplanktivorous seabird.

Marine Ecology Progress Series, 368, 295–304.