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The evolution of sensitive periods in development: insights from insects

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20 **Abstract**

21 Recent models have identified evolutionary explanations for sensitive periods, when individuals are
22 more responsive to experiences at certain stages of development, based on benefits and costs of
23 attending to environmental cues. Empirical tests of these models face challenges, requiring
24 complex, long-term experiments, and detailed understanding of physiology and ecology. Insect
25 systems offer the opportunity to overcome these challenges, given their tractability, diversity and
26 well-studied mechanisms. These studies shed light not only on fundamental biology, but have
27 societal implications given the roles insects play in pollinating or decimating food crops and in
28 spreading parasites. Understanding the role of sensitive periods can help to protect beneficial insect
29 populations while controlling pests and vectors of disease.

30

31 **Introduction**

32 Across most organisms, individuals receive inputs from their environment which may induce a
33 change in their behaviour, physiology or morphology. Such responses tend to be particularly strong
34 at certain life stages compared to others, often early in development, and can carry over to
35 influence phenotypes through the rest of life [1–3]. Examples of such sensitive periods abound
36 across the natural world. In humans, there are extensive studies showing how experiences of
37 challenging conditions, including environmental disaster, famine and social disruption, both *in utero*
38 and early in childhood, shape later coping strategies, behaviour and health [4–6]. In the Norway
39 spruce *Picea abies*, the temperature experienced during embryogenesis determines the height and
40 timing of bud set in the adult tree [7]; and studies in prairie voles *Microtus ochrogaster* show how
41 the amount and quality of parental care received as a pup influence later alloparenting, social bonds
42 and dispersal [8]. Many bird species learn their adult song in a critical window early in development:
43 in zebra finches *Taeniopygia guttata*, this period can be extended when they have delayed access
44 to an adult tutor but only if they already have a song template provided by hearing their father as a
45 young chick [9].

46

47 A long-standing question in evolutionary biology and developmental psychology is why individuals
48 would be particularly affected by experiences at certain stages of development (termed ‘sensitive
49 periods’ or ‘sensitive windows’) rather than exhibit the capacity to respond to the same extent to
50 their environment across their entire life course. Here, we first describe evolutionary models which
51 set out to ask how natural selection should favour the evolution of sensitive periods [10]. These
52 models present general insights into the adaptive basis of sensitive periods, and we discuss the
53 challenges empiricists face in testing model predictions. We argue that insect systems can be useful
54 for overcoming these challenges, owing to their experimental tractability and extensively studied
55 mechanisms. We end by describing examples from studies of sensitive periods on insect
56 pollinators, pests and vectors of disease to showcase the societal implications of such insights.

57

58 **Evolutionary models of sensitive periods**

59 In recent years, several theoretical models have investigated the conditions under which natural
60 selection would favour developmental programmes where individuals respond more to experiences
61 at certain life stages rather than others. The mechanics and key results of these models are clearly
62 summarised in a comprehensive review by Fawcett and Frankenhuis [10], and we briefly reiterate
63 these but refer readers to this review, follow-up studies and reviews [11–14], and the models therein
64 (e.g. Refs. [15–17]), for a more detailed presentation.

65

66 Most models exploring the evolution of sensitive periods are predicated on an information-based
67 perspective [10]. Individuals are constantly exposed to cues about their extrinsic environment or
68 their internal state, where ‘cues’ are observations that provide information (i.e., reduce uncertainty)
69 about the state of the world. By responding to these cues – adjusting their physiology or behaviour
70 – they potentially increase their reproductive value, or contribution to the next generation in the form
71 of evolutionary fitness. The cues individuals receive can vary in their reliability, or the degree to
72 which they reduce uncertainty about the environment. The extent to which individuals attend to
73 these cues may vary depending on their underlying confidence about the state of the world.
74 Moreover, individuals may be exposed to multiple cues which may differ in reliability. For example,

75 young individuals may be more influenced by their observation of adult responses to aversive
76 stimuli than by their own direct exposure to these stimuli.

77

78 Fawcett and Frankenhuis [10] summarise recent information-based models to highlight four main,
79 and not mutually exclusive, conditions under which individuals are particularly sensitive to cues at
80 certain stages of development. These are: first, when there is variation in the frequency (or
81 availability) of cues; second, when there is variation in the reliability of cues; third, when the fitness
82 value of responding to such cues is highest; and, fourth, when there are constraints on, or costs
83 resulting from, plasticity (i.e., the ability of a genotype to produce a range of phenotypes in response
84 to different environmental conditions) at other life stages. These four criteria are explained in more
85 detail in the section ‘Using insects to test sensitive periods evolution’ below.

86

87 While there is much to unpick in each of these criteria (see Refs. [10,13]), our aim here is to discuss
88 how empiricists can test these predictions. Models are, by definition, abstractions of reality
89 and, while yielding important insights into the operations of natural selection and guiding research
90 programmes, there are challenges in bridging model development and empirical testing. While this
91 is a general issue [18,19], there are particular challenges relating to the models of sensitive periods
92 and how to test them [13,14].

93

94 First, some models of the evolution of sensitive periods use simulations to recapitulate what
95 empiricists do, for example, by exposing individuals to experimental treatments [15] or adopting
96 them into different environments [13,17]. Setting up similar empirical experiments can be much
97 more challenging, however. If an experiment has set out to compare plasticity at different periods
98 during development, then a fully replicated design across different combinations is required, and
99 this can result in fairly large and unwieldy sample sizes.

100

101 Second, both individual phenotypes and environments are complex and multi-faceted, and
102 theoretical models cannot capture all this complexity, nor would it be useful for them to do so.

103 However, when faced with testing models, empiricists have to ask questions such as: what
104 environmental cue should be manipulated (e.g., temperature, population density, food availability),
105 and should a combination of such cues be considered [20]? Do we have data from natural
106 conditions on the reliability of these cues: for example, how might local encounters with conspecifics
107 indicate competition at the population level? Moreover, how do these cues reflect environmental
108 stability across development, as might be measured by statistics such as temporal autocorrelation
109 [14]? What behavioural or physiological response should be measured, for example, foraging,
110 exploratory behaviour, growth, sexual maturation, hormone production? While there are instances
111 where the relevant environmental cues are well established, and the relevant phenotypic adjustment
112 clearly connected to fitness outcomes, this represents a small minority of cases.

113

114 **Using insects to test the evolution of sensitive periods**

115 The challenges described above are not insurmountable, and we highlight how studies on insects
116 can provide a powerful means of understanding the evolution of sensitive periods. In so doing, we
117 reflect on existing studies which already provide useful insights yet, because of differences in
118 terminology, may not yet have been linked to the literature on sensitive periods. We acknowledge
119 that there is a wealth of literature on studying phenotypic plasticity in insects, from physiological
120 mechanism through to evolutionary adaptation (see Ref. [21] for an excellent introductory overview).
121 Classic examples include the dramatic change in appearance and behaviour of an individual desert
122 locust *Schistocerca gregaria* in response to increased conspecific density, which shifts from being
123 cryptic and avoiding conspecifics to exhibiting striking warning colouration and being attracted to its
124 neighbours [22]. Similarly, some populations of the soapberry bug adjust their mate-guarding
125 behaviour as an adaptive response to the sex ratio experienced during development, with males
126 guarding females more when they have experienced a male-biased sex ratio [23]. However, such
127 plasticity is only evident in populations which experienced variable sex ratios, whereas those with
128 more predictable encounter rates with females do not adjust their guarding behaviour as a
129 consequence of their experience.

130

131 In general, insect species kept in the laboratory are highly tractable experimental systems. They
132 have short lifespans, allowing the measurement of complete developmental trajectories within the
133 timeframe of most research programmes. In many insect model systems, behavioural phenotypes
134 are well characterised and can be measured with relative ease, even in the wild. Laboratory
135 populations can be kept under controlled conditions, which makes it possible to manipulate cues
136 across multiple stages of development (Figure 1) and to use of different types of cues. Large
137 populations can be monitored to quantify individual variability, and in well-characterised model
138 systems such as *Drosophila*, comparisons across genotypes can be used to assess genetic
139 variability in responsiveness to cues [24].

140

141 Importantly, in many insect models, the mechanisms underlying development are extremely well
142 established, including the transcription and translation of key genes and proteins, hormones and
143 signalling pathways involved in determining adult phenotype [25,26], and the role of DNA
144 methylation in determining the stability of responses within and across generations. For example,
145 the social and nutritional factors determining whether a *Pheidole* ant becomes a large or small
146 soldier are regulated by the rudimentary forewing disc, which determines the head to body size
147 scaling [27]. Similarly, the nature by which individuals sense their environment is often extremely
148 well characterised, such as how the sensory hairs on the legs of desert locusts allow detection of
149 conspecific density and trigger change to the gregarious morph (reference in Ref. [21]). Such
150 mechanistic insights could feed back into the evolutionary models, which have thus far been fairly
151 agnostic on mechanisms [13].

152

153 For comparative studies, insects provide a fascinating contrast in developmental mode (Figure 1).
154 Specifically, the distinction between hemimetabolous development, where nymphs proceed through
155 different developmental stages, without complete metamorphosis, and holometabolous
156 development, involving a complete morphological transition from larval form to an adult insect,
157 allows for key insights when considering insect systems in the context of sensitive periods in

development, as explained in further detail below. For further reading on the evolutionary relationships between these types of development, see Ref. [28].

Figure 1 Measuring sensitive periods in insect systems.

(a) Contrast between hemimetabolous and holometabolous insects, the latter undergoing a complete metamorphosis during the pupal stage (upper panel: Pacific beetle cockroach, *Diploptera punctata*; lower panel: winter moth, *Operophtera brumata*). **(b)** The type of experimental design used to study sensitive periods. Note that the type of cue (for example, temperature, food quality or quantity, predation, or social group density) applied in a hemimetabolous species is more likely to be similar across stages, whereas cues experienced at the larval and pupal stage in holometabolous insects are more likely to differ (as indicated by different colours; for example different types of food for the larva and adult winter moth).

We now turn to the four key predictions from models of the evolution of sensitive periods and assess existing empirical support from key insect studies.

175 First, Fawcett and Frankenhuis predict that there may be **certain periods of life when individuals**
176 **encounter cues about their environment more frequently than at other periods** [10]. In the
177 same way, there exist certain periods when individuals are not exposed to cues, such *in utero* when
178 mothers provide buffering from environmental adversity. In the context of insect systems, we can
179 draw a comparison between systems depending on the mode of development, with holometabolous
180 insects which undergo metamorphosis compared to hemimetabolous insects with more continuous
181 development (Figure 1).

182

183 In holometabolous insects, cues can vary dramatically across different life stages given the
184 extensive neurophysiological reorganisation involved in metamorphosis (Figure 1, bottom panel)
185 and highly contrasting levels of mobility between life stages, from immobile larvae to highly mobile
186 adults, with pupae being entirely sedentary and often left in protected micro-habitats. One might
187 then ask if and how the experience of cues at one stage of development can influence the
188 phenotype at later stages. In general, there is clear evidence for such effects and also for their
189 evolution, including a great diversity within and across species in how sensitive individuals are to
190 cues across development, and in the extent to which adult traits, such as size, longevity, fecundity
191 and behaviour, are affected by early-life cues (see Ref. [3] for more general discussion). In the case
192 of holometabolous insects, many studies consider how experiences limited to the larval stage
193 influence later adult traits. For example, larval density influences adult boldness and activity in the
194 leaf beetle *Phaedon cochleariae* [29]. Individuals reared in higher density are less bold, which may
195 be an adaptive strategy to avoid intra-specific conflict in this non-social species. Males reared in
196 higher density also have higher activity levels which can increase the chance of encountering
197 females. Chemical cues during larval development in the moth *Spodoptera littoralis* influence adult
198 host plant preference [30] or, in the ant *Aphaenogaster senilis* [31], the ability to recognise same-
199 colony individuals.

200

201 In hemimetabolous insects, it is more likely that cues are comparable across life stages and result in
202 more gradual adjustment in plasticity at different time points, consistent with predictions of Fawcett

203 and Frankenhuis, as there is no dramatic period of reorganisation and the sensory structure
204 remains similar across stages. Even in such systems, however, there is evidence for heightened
205 responses at early stages. In the Pacific beetle cockroach *Diploptera punctata*, for example, males
206 show accelerated development when reared in larger groups, but this effect is more likely to occur
207 when the exposed to social cues in the first stage of development than at later stages [32]. The
208 early maturation resulting from this accelerated development may enable early reproduction and so
209 represent a fitness advantage for these males (as relevant to the third prediction, described below).

210

211 A second prediction is that individuals will be more sensitive to their environment at periods when
212 **cues have higher reliability**. For example, parents may have better access to cues on
213 environmental risk than juveniles are able to gain for themselves; or cues on mate availability may
214 be more reliable at the point when individuals reach maturity. In insect systems, cue reliability and
215 how it changes across development can be easily assessed, particularly in those systems with
216 relatively short lifespans and where data from natural populations allow assessment of the extent to
217 which cues indicate fitness-relevant dimensions of the environment, as is required for testing
218 models [14]. For example, in burying beetles *Nicrophorus vespilloides*, larvae respond to the density
219 of phoretic mites on the carcass where they are reared as a cue of adult population density, and
220 field studies confirm the reliability of this cue [33]. Adults then adjust their reproductive investment if
221 they receive the same cue as adults, with those exposed to high mite density investing more in
222 current reproduction at a cost to survival, as this is potentially adaptive under a high-competition
223 environment [33].

224

225 Contrasting mobility across different developmental stages can generate differences in cue
226 reliability, and explain why certain life stages are more sensitive to experiences than others. For
227 example, in the kelp fly *Paractora dreuxi*, larvae exhibit rapid cold hardening, a physiological
228 mechanism to survive otherwise lethal cold temperatures, after previous exposure to cold
229 temperatures (a predictable cue for this immobile stage), whereas highly mobile adults do not
230 exhibit this response, as they can experience a wide range of temperatures [34].

231

232 Third, Fawcett and Frankenhuis predict that the **fitness benefits of responding to cues** may vary
233 depending on when these cues are received. For example, if complex phenotypes take time to
234 develop, then responding to cues early in life may garner greater fitness advantages than when the
235 response is initiated later. For most insect species, individuals can be followed across their whole
236 lifespan, allowing researchers to record both when environmental cues (such as temperature,
237 nutrition or population density) were perceived, and when phenotypes were produced, including
238 data on survival, reproduction and transgenerational effects. This enables researchers studying
239 insect systems to connect the dots between cues at specific periods and eventual fitness outcomes.
240 Experimental studies on the winter moth, *Operophtera brumata*, for example, show that individuals
241 adjust the duration of the pupal period in response to photoperiod cues experienced as a newly
242 hatched larva [35]. Such adjustments to early-life cue exposure can increase fitness, allowing adults
243 to emerge at the same time (an observation supported by long-term field data [35]) – even when
244 eggs have hatched at different times owing to optimal larval food availability. This could maximize
245 mating opportunities given that females are flightless and the benefit of synchronisation in terms of
246 mate location potentially trumps any cost in terms of competition. In the ant *Camponotus floridanus*,
247 the ability of larvae to respond to chemical cues and hormones provided by adults during rearing is
248 essential as responding to such cues leads to larger adult body size and an increased likelihood of
249 surviving metamorphosis [36], both of which indicate the ant colony's fitness.

250

251 Fourth, sensitive periods during development can evolve when certain life stages experience strong
252 **constraints on plasticity, or high costs of responding**, even if individuals are exposed to cues.
253 The determination of body size in holometabolous insects provides strong support for this
254 prediction, whereby the amount of food ingested during the larval stage is key for deciding the size
255 of the adult insect, and because of the hard exoskeleton subsequent growth is not possible, even if
256 more food is available (indeed, in many lepidopteran species the adult stage does not feed at all)
257 [21]. Similarly, in holometabolous insects, larvae are less mobile than adults, and pupae do not
258 move at all. This limits their ability to escape from unfavourable temperatures, leading to the

259 prediction that thermal plasticity is higher in the larval and pupal stage than later adult stages, as
260 these immobile stages have to exhibit more thermal tolerance when they cannot move away [37].
261 Such stage-dependent thermal plasticity has been found in the fruit feeding butterfly *Bicyclus*
262 *anyana* [38] and the kelp fly [34]. Considering such stage-dependent plasticity is key when
263 comparing the thermal performance of insect populations experiencing different thermal regimes
264 [39], yet many studies only measure plastic responses in adults.

265

266 **Importance of sensitive periods in insects**

267 Understanding the evolution of sensitive periods can have ramifications beyond fundamental
268 biology, given the important role many insect species play as pollinators, pests and disease vectors.

269

270 There is global concern about declining pollinator populations, which are key for human food
271 security given our reliance on insect-pollinated crops. Sensitive periods in development play a
272 critical role in understanding the biology and conservation of these species: honeybees are a
273 textbook example for how components in the diet determine the developmental fate of an individual
274 – whether as a worker or a queen ([40], references in Ref. [41]). The dire consequences of
275 exposure to neonicotinoid pesticides can vary depending on the developmental stage of exposure,
276 with studies in solitary bees showing that larval stages may be less susceptible than adults [42] in
277 terms of survival. Nevertheless, larval exposure to these substances, in bumblebees, can affect
278 adult brain morphology and reduce learning performance [43].

279

280 Understanding sensitive periods also plays a role in predicting and controlling the spread of crop
281 pests. Recent work by Tarusikirwa *et al.* in the tomato leaf miner *Tuta absoluta*, a major global pest
282 of tomato plants, has shown that larval stages have higher thermal plasticity and tolerance than
283 their adult counterparts, illustrating the role of key life stages in enabling the success of this species
284 at invading new environments [44]. Similarly, thermal tolerance is higher in nymphs than adults of
285 the English grain aphid *Sitobion avenae*, a major pest of wheat crops, most probably because

adults are avoiding reproduction or survival costs of thermal responses and because they can thermoregulate using behavioural means [45].

Mosquitoes are a major vector of malaria parasites, causing over 400,000 deaths per year, >90 per cent of these on the African continent [46]. Mosquito species have holometabolous development, and mosquito larvae often develop in ephemeral pools of stagnant water, during which time they acquire nutrients which determine later body size [47], avoid predation and parasites, and time their maturity in order to have long enough to develop into a large size, but not so long that they face desiccation. There are consequences of variation in the environment during these sensitive periods on mosquito ability to transmit parasites (termed ‘vector competence’) [48,49], immunity [50] and insecticide resistance [51]. Interactions between multiple stressors, including heat stress, low nutrition or exposure to insecticide, can modulate the importance of this sensitive period on adult size [47], which is linked to fecundity, or adult immunity [50], and can affect vector competence and survival. This sensitive period could be directly targeted by using larval insecticides or parasites, by introducing predator fish or by draining and fragmenting larval habitats. This may lead to the emergence of certain adult phenotypes, if they survive these larval control measures, which exhibit decreased insecticide resistance or longevity [52–55]. A better understanding of how sensitive periods shape mosquito population dynamics and adult vectorial capacity – which is a result of mosquito biting rate, longevity, immunity and vector competence – will thus facilitate the prediction of mosquito-borne disease transmission and also improve local mosquito control strategies.

When considering the link between sensitive periods and public health, another disease vector of interest is the tsetse fly (*Glossina* species), vector of trypanosome parasites, which cause debilitating disease in humans, livestock and animals across sub-Saharan Africa. With their unusual life history, tsetse present an interesting model system for the study of sensitive periods. Tsetse females give birth to live offspring, which emerge the same size as the mother [56], thus the larva receives cues and inputs entirely through its mother. There has been considerable research into the effects of temperature at different stages of development on adult size [57,58], survival [59] and

consequences for population dynamics [60]. It remains unclear, however, whether cues or stressors during the larval stage (*in utero*) have a stronger effect on adult phenotype than those at later stages (pupal, or early adult) and, if so, the mechanisms and adaptive nature of these effects. The field is thus ripe for experiments exploring the relative influence of these varying stressors across development, and their consequences for fly behaviour and disease spread [61]. The sensitive period of development *in utero* could be exploited for tsetse control by disrupting maternal allocation either of nutrients or, powerfully, by manipulating the maternally derived symbiotic bacteria, which are essential for vitamin synthesis with consequences for fecundity, longevity and immunity [62,63]. Recent work has shown that it is possible genetically to modify these symbiotic bacteria to reduce longevity and fecundity, and inject them into late-stage larvae *in utero* so that they can then be transmitted vertically to offspring [64]. Whether such techniques can be scaled up to reduce tsetse populations under field settings has yet to be established but could yield an exciting prospect for controlling this important disease vector.

Conclusions

Theoretical models allow us to formalize questions about why sensitive periods might be favoured by natural selection, but there is still a gap between theory and empirical examples. Insects represent a powerful group of species to test theoretical models and inspire new ones, given their tractability, knowledge of developmental mechanisms and their relatively short lifespan which enables multigenerational studies. Indeed, multiple studies already exist, yet have not been linked to the sensitive period modelling work, probably because of the use of different terminology. In highlighting some of these studies, we hope to encourage further empirical studies informed by theory, and theoretical studies inspired by insect life cycle diversity and mechanistic insights. Such an interplay between theory and empirical testing is not only of fundamental interest but can be relevant to our health and well-being, for example by improving our understanding of insect vectors of disease.

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348

349 References

- 350 1. Lindström J: **Early development and fitness in birds and mammals.** *Trends Ecol Evol* 1999,
351 **14**:343–348.
- 352 2. Monaghan P: **Early growth conditions, phenotypic development and environmental**
353 **change.** *Philos Trans R Soc Lond B Biol Sci* 2008, **363**:1635–45.
- 354 3. Moore MP, Martin RA: **On the evolution of carry-over effects.** *J Anim Ecol* 2019, **88**:1832–
355 1844.
- 356 4. Almas AN, Papp LJ, Woodbury MR, Nelson CA, Zeanah CH, Fox NA: **The impact of**
357 **caregiving disruptions of previously institutionalized children on multiple outcomes in**
358 **late childhood.** *Child Dev* 2020, **91**:96–109.
- 359 5. Duchesne A, Liu A, Jones SL, Laplante DP, King S: **Childhood body mass index at 5.5 years**
360 **mediates the effect of prenatal maternal stress on daughters' age at menarche: Project**
361 **Ice Storm.** *J Dev Orig Health Dis* 2017, **8**:168–177.
- 362 6. Schulz LC: **The Dutch Hunger Winter and the developmental origins of health and**
363 **disease.** *Proc Natl Acad Sci* 2010, **107**:16757–8.
- 364 7. Kvaalen H, Johnsen Ø: **Timing of bud set in *Picea abies* is regulated by a memory of**
365 **temperature during zygotic and somatic embryogenesis.** *New Phytol* 2008, **177**:49–59.
- 366 8. Perkeybile AM, Bales KL: **Intergenerational transmission of sociality: the role of parents in**
367 **shaping social behavior in monogamous and non-monogamous species.** *J Exp Biol* 2017,
368 **220**:114–123.
- 369 9. Gobes SMH, Jennings RB, Maeda RK: **The sensitive period for auditory-vocal learning in**
370 **the zebra finch: Consequences of limited-model availability and multiple-tutor paradigms**
371 **on song imitation.** *Behav Processes* 2019, **163**:5–12.
- 372 10. Fawcett TW, Frankenhuis WE: **Adaptive explanations for sensitive windows in**
373 **development.** *Front Zool* 2015, **12**:S3.
- 374 11. Stamps JA, Krishnan VV: **Age-dependent changes in behavioural plasticity: insights from**
375 **Bayesian models of development.** *Anim Behav* 2017, **126**:53–67.
- 376 12. Stamps JA, Frankenhuis WE: **Bayesian models of development.** *Trends Ecol Evol* 2016,
377 **31**:260–268.

- 378 13. Frankenhuis WE, Walasek N: **Modeling the evolution of sensitive periods.** *Dev Cogn*
379 *Neurosci* 2020, **41**:100715.
- 380 14. Frankenhuis Willem E., Nettle Daniel, Dall Sasha R. X.: **A case for environmental statistics of**
381 **early-life effects.** *Philos Trans R Soc B Biol Sci* 2019, **374**:20180110.
- 382 15. English S, Fawcett TW, Higginson AD, Trimmer PC, Uller T: **Adaptive use of information**
383 **during growth can explain long-term effects of early life experiences.** *Am Nat* 2016,
384 **187**:620–632.
- 385 16. Frankenhuis WE, Panchanathan K: **Balancing sampling and specialization: an adaptationist**
386 **model of incremental development.** *Proc R Soc B* 2011, **278**:3558–65.
- 387 17. Panchanathan K, Frankenhuis WE: **The evolution of sensitive periods in a model of**
388 **incremental development.** *Proc R Soc B Biol Sci* 2016, **283**:20152439.
- 389 18. Otto SP, Rosales A: **Theory in service of narratives in evolution and ecology.** *Am Nat* 2020,
390 **195**:290–299.
- 391 19. Servedio MR, Brandvain Y, Dhole S, Fitzpatrick CL, Goldberg EE, Stern CA, Cleve JV, Yeh DJ:
392 **Not just a theory—the utility of mathematical models in evolutionary biology.** *PLOS Biol*
393 2014, **12**:e1002017.
- 394 20. Mueller CA: **Critical windows in animal development: interactions between environment,**
395 **phenotype, and time.** In *Development and Environment*. Edited by Burggren W, Dubansky B.
396 Springer International Publishing; 2018:41–72.
- 397 21. Whitman DW, Agrawal AA: **What is phenotypic plasticity and why is it important?** In
398 *Phenotypic Plasticity of Insects: Mechanisms and Consequences*. Edited by Whitman DW,
399 Ananthakrishnan TN. Science Publishers; 2009.
- 400 22. Ayali A: **The puzzle of locust density-dependent phase polyphenism.** *Curr Opin Insect Sci*
401 2019, **35**:41–47.
- 402 23. Carroll SP, Corneli PS: **Divergence in male mating tactics between two populations of the**
403 **soapberry bug: II. Genetic change and the evolution of a plastic reaction norm in a**
404 **variable social environment.** *Behav Ecol* 1995, **6**:46–56.
- 405 24. Stamps JA, Biro PA, Mitchell DJ, Saltz JB: **Bayesian updating during development predicts**
406 **genotypic differences in plasticity.** *Evolution* 2018, **72**:2167–2180.
- 407 25. Koyama T, Mirth CK: **Unravelling the diversity of mechanisms through which nutrition**
408 **regulates body size in insects.** *Curr Opin Insect Sci* 2018, **25**:1–8.
- 409 26. Nijhout HF, McKenna KZ: **The distinct roles of insulin signaling in polyphenic**
410 **development.** *Curr Opin Insect Sci* 2018, **25**:58–64.
- 411 27. Rajakumar R, Koch S, Couture M, Favé M-J, Lillico-Ouachour A, Chen T, De Blasis G,
412 Rajakumar A, Ouellette D, Abouheif E: **Social regulation of a rudimentary organ generates**
413 **complex worker-caste systems in ants.** *Nature* 2018, **562**:574–577.
- 414 28. Jindra M: **Where did the pupa come from? The timing of juvenile hormone signalling**
415 **supports homology between stages of hemimetabolous and holometabolous insects.**
416 *Philos Trans R Soc B Biol Sci* 2019, **374**:20190064.

- 417 29. Müller T, Küll CL, Müller C: **Effects of larval versus adult density conditions on**
418 **reproduction and behavior of a leaf beetle.** *Behav Ecol Sociobiol* 2016, **70**:2081–2091.
- 419 30. Proffitt M, Khallaf MA, Carrasco D, Larsson MC, Anderson P: **‘Do you remember the first**
420 **time?’ Host plant preference in a moth is modulated by experiences during larval feeding**
421 **and adult mating.** *Ecol Lett* 2015, **18**:365–374.
- 422 31. Signorotti L, Jaisson P, d’Ettorre P: **Larval memory affects adult nest-mate recognition in**
423 **the ant *Aphaenogaster senilis*.** *Proc R Soc B Biol Sci* 2014, **281**:20132579.
- 424 32. Holbrook G, Schal C: **Social influences on nymphal development in the cockroach,**
425 ***Diploptera punctata*.** *Physiol Entomol* 1998, **23**:121–130.
- 426 33. De Gasperin O, Duarte A, English S, Attisano A, Kilner RM: **The early-life environment and**
427 **individual plasticity in life-history traits.** *Ecol Evol* 2019, **9**:339–351.
- 428 34. Terblanche JS, Marais E, Chown SL: **Stage-related variation in rapid cold hardening as a**
429 **test of the environmental predictability hypothesis.** *J Insect Physiol* 2007, **53**:455–462.
- 430 35. Salis L, Hoorn E van den, Beersma DGM, Hut RA, Visser ME: **Photoperiodic cues regulate**
431 **phenological carry-over effects in an herbivorous insect.** *Funct Ecol* 2018, **32**:171–180.
- 432 36. LeBoeuf AC, Waridel P, Brent CS, Gonçalves AN, Menin L, Ortiz D, Riba-Grognuz O, Koto A,
433 Soares ZG, Privman E, et al.: **Oral transfer of chemical cues, growth proteins and**
434 **hormones in social insects.** *eLife* 2016, **5**:e20375.
- 435 37. Huey RB, Hertz PE, Sinervo B: **Behavioral drive versus behavioral inertia in evolution: a**
436 **null model approach.** *Am Nat* 2003, **161**:357–66.
- 437 38. Klockmann M, Günter F, Fischer K: **Heat resistance throughout ontogeny: body size**
438 **constrains thermal tolerance.** *Glob Change Biol* 2017, **23**:686–696.
- 439 39. MacLean HJ, Higgins JK, Buckley LB, Kingsolver JG: **Geographic divergence in upper**
440 **thermal limits across insect life stages: does behavior matter?** *Oecologia* 2016, **181**:107–
441 114.
- 442 40. Mao W, Schuler MA, Berenbaum MR: **A dietary phytochemical alters caste-associated gene**
443 **expression in honey bees.** *Sci Adv* 2015, **1**:e1500795.
- 444 41. English S, Browning LE, Raihani NJ: **Developmental plasticity and social specialization in**
445 **cooperative societies.** *Anim Behav* 2015, **106**:37–42.
- 446 42. Nicholls E, Fowler R, Niven JE, Gilbert JD, Goulson D: **Larval exposure to field-realistic**
447 **concentrations of clothianidin has no effect on development rate, over-winter survival or**
448 **adult metabolic rate in a solitary bee, *Osmia bicornis*.** *PeerJ* 2017, **5**:e3417.
- 449 43. Smith DB, Arce AN, Ramos Rodrigues A, Bischoff PH, Burris D, Ahmed F, Gill RJ: **Insecticide**
450 **exposure during brood or early-adult development reduces brain growth and impairs**
451 **adult learning in bumblebees.** *Proc R Soc B Biol Sci* 2020, **287**:20192442.
- 452 44. Tarusikirwa VL, Mutamiswa R, English S, Chidawanyika F, Nyamukondiwa C: **Thermal**
453 **plasticity in the invasive south American tomato pinworm *Tuta absoluta* (Meyrick)**
454 **(Lepidoptera: Gelechiidae).** *J Therm Biol* 2020, **90**:102598.

- 455 45. Zhao F, Hoffmann AA, Xing K, Ma C: **Life stages of an aphid living under similar thermal**
456 **conditions differ in thermal performance.** *J Insect Physiol* 2017, **99**:1–7.
- 457 46. World Health Organisation: *World malaria report 2019*. WHO; 2019.
- 458 47. Barreaux AMG, Stone CM, Barreaux P, Koella JC: **The relationship between size and**
459 **longevity of the malaria vector *Anopheles gambiae* (s.s.) depends on the larval**
460 **environment.** *Parasit Vectors* 2018, **11**:485.
- 461 48. Barreaux AMG, Barreaux P, Thiévent K, Koella JC: **Larval environment influences vector**
462 **competence of the malaria mosquito *Anopheles gambiae*.** *MalariaWorld J* 2016, **7**:8.
- 463 49. Vantaux A, Lefèvre T, Cohuet A, Dabiré KR, Roche B, Roux O: **Larval nutritional stress**
464 **affects vector life history traits and human malaria transmission.** *Sci Rep* 2016, **6**:1–10.
- 465 50. Hauser G, Koella JC: **Larval exposure to a pyrethroid insecticide and competition for food**
466 **modulate the melanisation and antibacterial responses of adult *Anopheles gambiae*.** *Sci*
467 *Rep* 2020, **10**:1–8.
- 468 51. Owusu HF, Chitnis N, Müller P: **Insecticide susceptibility of *Anopheles* mosquitoes**
469 **changes in response to variations in the larval environment.** *Sci Rep* 2017, **7**:1–9.
- 470 52. Koella JC, Lynch PA, Thomas MB, Read AF: **Towards evolution-proof malaria control with**
471 **insecticides.** *Evol Appl* 2009, **2**:469–480.
- 472 53. Lorenz LM, Koella JC: **The microsporidian parasite *Vavraia culicis* as a potential late life–**
473 **acting control agent of malaria.** *Evol Appl* 2011, **4**:783–790.
- 474 54. Koella JC, Saddler A, Karacs TPS: **Blocking the evolution of insecticide-resistant malaria**
475 **vectors with a microsporidian.** *Evol Appl* 2012, **5**:283–292.
- 476 55. Gowelo S, Chirombo J, Spitzen J, Koenraad CJM, Mzilahowa T, van den Berg H, Takken W,
477 McCann R: **Effects of larval exposure to sublethal doses of *Bacillus thuringiensis* var.**
478 **israelensis on body size, oviposition and survival of adult *Anopheles coluzzii***
479 **mosquitoes.** *Parasit Vectors* 2020, **13**:259.
- 480 56. Leak SG: *Tsetse Biology and Ecology: Their Role in the Epidemiology and Control of*
481 *Trypanosomiasis*. ILRI (aka ILCA and ILRAD); 1999.
- 482 57. English S, Cowen H, Garnett E, Hargrove JW: **Maternal effects on offspring size in a natural**
483 **population of the viviparous tsetse fly.** *Ecol Entomol* 2016, **41**:618–626.
- 484 58. Hargrove JW, Muzari MO, English S: **How maternal investment varies with environmental**
485 **factors and the age and physiological state of wild tsetse *Glossina pallidipes* and**
486 ***Glossina morsitans morsitans*.** *R Soc Open Sci* 2018, **5**:171739.
- 487 59. Hargrove JW, Vale GA: **Models for the rates of pupal development, fat consumption and**
488 **mortality in tsetse (*Glossina* spp).** *Bull Entomol Res* 2020, **110**:44–56.
- 489 60. Lord JS, Hargrove JW, Torr SJ, Vale GA: **Climate change and African trypanosomiasis**
490 **vector populations in Zimbabwe's Zambezi Valley: A mathematical modelling study.**
491 *PLOS Med* 2018, **15**:e1002675.
- 492 61. English S, Barreaux AMG, Bonsall MB, Hargrove JW, Keeling MJ, Rock KS, Vale GA:
493 **Incorporating vector ecology and life history into disease transmission models: insights**

- 494 **from tsetse (*Glossina* spp.).** In *Population Biology of Vector-Borne Diseases*. . Oxford
 495 University Press; In press.
- 496 62. Benoit JB, Attardo GM, Baumann AA, Michalkova V, Aksoy S: **Adenotrophic viviparity in**
 497 **tsetse flies: potential for population control and as an insect model for lactation.** *Annu*
 498 *Rev Entomol* 2015, **60**:351–371.
- 499 63. Michalkova V, Benoit JB, Weiss BL, Attardo GM, Aksoy S: **Vitamin B6 generated by obligate**
 500 **symbionts is critical for maintaining proline homeostasis and fecundity in tsetse flies.**
 501 *Appl Environ Microbiol* 2014, **80**:5844–5853.
- 502 64. De Vooght L, Van Keer S, Van Den Abbeele J: **Towards improving tsetse fly**
 503 **paratransgenesis: stable colonization of *Glossina morsitans morsitans* with genetically**
 504 **modified *Sodalis*.** *BMC Microbiol* 2018, **18**:165.

505

506 **Annotated references:**

- 507 *13. Frankenhuys WE, Walasek N: **Modeling the evolution of sensitive periods.** *Dev Cogn*
 508 *Neurosci* 2020, **41**:100715.

509 Recent review of the models on the evolution of sensitive periods, highlighting the general findings
 510 and insights of most relevance to cognitive neuroscience. Gives a clear overview of the different
 511 model paradigms and assumptions, and discusses challenges of bridging theory and empirical
 512 work.

513

- 514 *20. Mueller CA: **Critical windows in animal development: interactions between environment,**
 515 **phenotype, and time.** In *Development and Environment*. Edited by Burggren W, Dubansky B.
 516 Springer International Publishing; 2018:41–72.

517 An overview of critical windows during development, with examples mainly drawn from amphibians
 518 and fish. Discusses complexities of experiments to measure critical windows, requiring different
 519 stressors, multiple windows across development and variable exposures. Proposes a 3D landscape
 520 design to deal with this complexity.

521

- 522 *24. Stamps JA, Biro PA, Mitchell DJ, Saltz JB: **Bayesian updating during development predicts**
 523 **genotypic differences in plasticity.** *Evolution* 2018, **72**:2167–2180.

524 Shows the power of insect model systems to test recent Bayesian models of development. Here,
 525 larvae from 116 different *Drosophila melanogaster* genotypes, varying in their initial preference for,
 526 or aversion to, the odour of ethyl acetate, were given aversive experiences of this odour. In line with
 527 model predictions, variance in responses declines after the aversive experience, with those
 528 genotypes having a stronger initial preference showing a greater decline in response.

529

- 530 *27. Rajakumar A, Ouellette D, Abouheif E: **Social regulation of a rudimentary organ generates**
 531 **complex worker-caste systems in ants.** *Nature* 2018, **562**:574–577.

532 Uses micro-dissection and RNA-interference to elucidate the mechanisms by which larvae become
 533 small or large soldiers in *Pheidole* ants. Graphic model explains how both nutrition and social cues
 534 initiate the process of caste determination, involving juvenile hormone and growth of rudimentary
 535 wing discs.

536

537 *35. Salis L, Hoorn E van den, Beersma DGM, Hut RA, Visser ME: **Photoperiodic cues regulate**
538 **phenological carry-over effects in an herbivorous insect.** *Funct Ecol* 2018, **32**:171–180.

539 Uses both long-term field data and an experiment in the winter moth to show how individuals adjust
540 developmental timing according to early-life cues. In this case, pupal duration depends on
541 photoperiod experienced as a newly hatched larva. This likely has important fitness consequences:
542 fine-tuning of pupal timing allows adults to emerge synchronously, thus maximising mating
543 opportunities and lining up their development with host plant phenology.
544