

REVIEW

Causes and Consequences of Phenotypic Plasticity

The evolution of sensitive periods beyond early ontogeny: Bridging theory and data

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Abstract

1. Sensitive periods, in which experiences have a large impact on phenotypic development, are most common early in ontogeny. Yet, they may also occur at later ontogenetic stages, such as adolescence. At present, however, we know little about why natural selection favours sensitive periods for some traits early in ontogeny and for others later in ontogeny. This article synthesizes recent mathematical models and empirical studies that explore sensitive periods beyond early ontogeny.
2. Across mathematical models, we observe two general patterns. First, sensitive periods emerge beyond early ontogeny when an organism's uncertainty about the environment-phenotype fit increases at later developmental stages. Second, sensitive periods emerge beyond early ontogeny when cues at later stages reduce this uncertainty more than earlier cues do.
3. In the empirical literature, we observe that traits showing sensitive periods beyond early ontogeny tend to be social traits, particularly among mammals. Connecting theory to data, we hypothesize that mammals have evolved to expect reliable information from peers in adolescence to reduce uncertainty about the current and future social environment (e.g. social dominance, mate value).
4. Finally, we highlight current gaps in our understanding and suggest future directions for strengthening bridges between empirical and theoretical studies of sensitive periods. Ultimately, we hope our synthesis will contribute towards an integrative science of sensitive periods across the biological and the social sciences.

KEYWORDS

adolescence, development, evolution, modelling, phenotypic plasticity, sensitive periods

1 | PLASTICITY BEYOND EARLY ONTOGENY

Phenotypic plasticity—the ability of organisms to adjust their phenotypes in response to environmental conditions and physiological

states (West-Eberhard, 2003)—is common early in ontogeny, yet it may also exist at later developmental stages, such as adolescence. High levels of plasticity in adolescence and adulthood have been documented across taxa, including primates, rodents, birds (Fuchs & Flügge, 2014), reptiles, amphibians (Powers, 2016), fish

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(Ganz & Brand, 2016), and insects (Eriksson et al., 2019; Strambi et al., 1999).

The existence of plasticity beyond early ontogeny raises a question: has plasticity merely persisted from earlier developmental stages, or is there a spike in plasticity later in ontogeny, implying a sensitive period? It is difficult to differentiate these possibilities empirically (Fuhrmann et al., 2015). Regardless, and contrary to some claims (Fuchs & Flügge, 2014), these cases clearly show that plasticity does not always diminish early in ontogeny. In this article, we ask whether and how evolutionary selection pressures cause variation in plasticity beyond early ontogeny across species, individuals, and traits.

1.1 | Understanding sources of variation in sensitive periods

In the past decades, there is growing interest in the genetic, neurophysiological, and environmental causes of variation in levels of plasticity. For example, geneticists have highlighted mechanisms that regulate the ontogenetic timing of sensitivity to information available to developing organisms ('cues') (Rundle & Spicer, 2016). Neuroscientists have uncovered the neurophysiological mechanisms underlying variation in sensitive periods (Gabard-Durnam & McLaughlin, 2020). And biologists have shown how environmental conditions and physiological states during development shape the features of sensitive periods, such as their timing and duration (Knudsen, 2004). These literatures have focused more on proximate mechanisms, studying *how* sensitive periods are instantiated, and less on ultimate selection pressures, studying *why* such periods have evolved.

As Niko Tinbergen (1963) argued, a complete explanation requires linking proximate (mechanisms, development) and ultimate levels (function, evolutionary history) (Bateson & Laland, 2013; Bergman & Beehner, 2022). To illustrate, consider an example in guinea pigs. Housing conditions during adolescence (i.e. living in pairs or in colonies) shape their levels of stress and aggression in adulthood to a larger extent than housing conditions during other life stages (Sachser et al., 2018, 2020). This plasticity in adolescence appears to be functional, because it enables guinea pigs to adjust to fluctuations in the social environment, such as changes in the density of male competitors (Sachser et al., 2018). But which environmental conditions could have selected for this pattern over evolutionary time? It is known that the ancestral species of the domestic guinea pig, the wild cavy, experiences drastic, yearly fluctuations in population size and composition (Sachser et al., 2018). To understand whether this variation can explain guinea pigs' heightened plasticity to the social environment in adolescence, it would be informative to draw on more general theory. In this paper, we, therefore, discuss recent mathematical models exploring the emergence of sensitive periods beyond early ontogeny.

1.2 | Modelling the evolution of sensitive periods

There is a longstanding and well-developed theoretical tradition studying the conditions that favour phenotypic plasticity versus non-plastic strategies (Botero et al., 2015; Snell-Rood & Steck, 2019; Stephens, 1991) as well as reversible or irreversible plasticity (Gabriel, 2006; Piersma & Drent, 2003). But theoreticians have only recently explored why and how levels of plasticity change across ontogeny (reviewed in Fawcett & Frankenhuis, 2015; Frankenhuis & Fraley, 2017; Frankenhuis & Walasek, 2020; Stamps & Luttbegg, 2022). This work provides insights into the effects of experience on the characteristics of sensitive periods, including their timing and duration. These models advance our understanding of *why* variation in sensitive periods exists, complementing research on *how* it is instantiated through (epi)genetic, neurophysiological, and developmental processes.

Models of sensitive periods typically conceptualize development as a sequential decision-making process. Organisms are conceived or born with a prior estimate about their environment (e.g. safe or dangerous). Organisms sample cues across ontogeny that provide imperfect knowledge about the environmental state, changing their information state (Stamps & Frankenhuis, 2016). The extent to which cues accurately reflect environmental conditions is often called the 'cue reliability' (or 'cue validity'). Some models additionally consider how changes in the information state (e.g. increased estimate about the presence of predators) map onto phenotypic adjustments (e.g. development of defences) (e.g. Fischer et al., 2014; Frankenhuis & Panchanathan, 2011; Walasek et al., 2022a, 2022b). These models then compute optimal trajectories that maximize survival and reproductive success (i.e. biological fitness). A robust finding across models is that plasticity tracks an organism's uncertainty about the environment: The higher this uncertainty is at conception or birth and the more prenatal and postnatal cues reduce it, the higher plasticity tends to be early in ontogeny, relative to later life stages (Fawcett & Frankenhuis, 2015; Frankenhuis & Fraley, 2017; Frankenhuis & Walasek, 2020).

2 | THEORETICAL SYNTHESIS

Although most mathematical models find sensitive periods early in ontogeny, recent models point to conditions that favour sensitive periods later in ontogeny (Fischer et al., 2014; Stamps & Krishnan, 2017; Walasek et al., 2022a, 2022b). It is not yet clear whether later sensitive periods are produced by the same or different selection pressures as early sensitive periods. Here, we address this question by synthesizing findings across models. We include models in our analysis if they meet three criteria. First, organisms use cues to learn about their environment. Second, the model captures changes in plasticity across ontogeny, including two or more time periods in which organisms can access cues. Third, the model produces sensitive periods beyond early ontogeny; that is, the highest

levels of plasticity towards the middle or end of ontogeny, rather than at the onset of ontogeny (the typical pattern). We have found four models that meet these criteria (Fischer et al., 2014; Stamps & Krishnan, 2017; Walasek et al., 2022a, 2022b).

Our synthesis focuses on adaptive explanations for sensitive periods occurring later in ontogeny. If a model also produces sensitive periods at the onset of ontogeny in a subset of conditions, we may discuss those for contrast. Additionally, we collected empirical examples of sensitive periods later in ontogeny in human and non-human animals (Table 1). As with the models, we only consider examples in which animals learn from cues over multiple time periods and show their highest levels of plasticity later in ontogeny. These examples represent sensitive periods beyond early ontogeny that we could identify and match with our theoretical explanations implied by the models. There may well exist other, suitable examples. We hope that our synthesis encourages others to identify empirical studies that we have missed.

The immediate goal of our synthesis is to review and link theoretical and empirical studies reporting sensitive periods beyond early ontogeny. In the long term, we hope that this synthesis stimulates future discourse about sensitive periods beyond early ontogeny. In the discussion section, we suggest concrete future directions based on our findings which can foster such a discourse. These directions include novel observational and experimental studies for identifying sensitive periods beyond early ontogeny, as well as modelling extensions that incorporate empirical insights.

2.1 | Scope of synthesis

In this paper, we use the term 'ontogeny' to denote the time window in which cues (i.e. experiences that provide information) are relevant to the development of traits. Thus, we refer to the ontogeny of a specific trait and not necessarily to the ontogeny of the organism

TABLE 1 Empirical examples of sensitive periods beyond early ontogeny. Columns indicate the species, trait, pattern (midway vs. end of ontogeny), the (ultimate) theoretical explanation that best fits the example, and the associated reference. For some studies it is unclear whether they capture a sensitive period towards the end of ontogeny or persisting plasticity, following an earlier peak. In these cases, we list both patterns.

Species	Trait	Timing of sensitive periods	Theoretical explanation	Reference
Humans	Stress recalibration in response to adoption	Midway	Increasing uncertainty	DePasquale et al. (2021), Gunnar et al. (2019)
Humans	Increased information sampling in response to increased uncertainty	Midway	Increasing uncertainty	Ma et al. (2022)
Chimpanzees	Increased social exploration and learning in response to novel social landscapes and independence from parents	Midway	Increasing uncertainty	Reviewed in Reddy et al. (2022)
Fish (Amazon molly, <i>Poecilia formosa</i>)	Behaviour in fish tanks (i.e. step length, turning angle, and distance to the tank wall)	Midway	Increasing uncertainty	Ehlman, Scherer, Bierbach, Stärk, et al. (2023)
Humans	Susceptibility to social feedback from peers	Midway	Increasing cue reliability	Molleman et al. (2022) and reviewed in Hofmans and van den Bos (2022)
Various rodent species	Changes in aggression, exploration, and social play behaviour in response to social defeat and housing conditions	Midway	Increasing cue reliability	Reviewed in Sachser et al. (2018)
Various rodent species	Social, anxiety-like, cognitive, and decision-making behaviours in response to social isolation	Midway	Increasing cue reliability	Reviewed in Li et al. (2021)
Bulb mites (<i>Rhizoglyphus robini</i>)	Male morph development in response to body size	End	Changing environment	Leigh and Smallegange (2014), Smallegange (2011)
Waterflea (<i>Daphnia magna</i>)	Size at maturity in response to short-term exposure to predator kairomones	End	Changing environment	Mikulski and Pijanowska (2010)
Paper wasps (<i>Polistes dominula</i>)	Nest-mate recognition in response to olfactory cues	End	Changing environment	Cappa et al. (2020)
Guinea pigs (<i>Cavia aperea f. porcellus</i>)	Changes in endocrine mechanisms (testosterone and cortisol concentrations) in response to niche transition	End or persisting plasticity	Changing environments	Mutwill et al. (2019, 2020)
Various rodent species	Changes in social behaviour and brain physiology in response to stress caused by changing, social environments	End or persisting plasticity	Changing environments	MacLeod et al. (2023)

(i.e. the whole period during which an organism develops). The onset of 'trait ontogeny' does not necessarily coincide with conception or birth; animals might only be able to develop some traits at later life stages due to physiological constraints or because relevant cues are not available yet (Fawcett & Frankenhuis, 2015; Stamps & Luttbeg, 2022). Figure S1 illustrates the relationship between trait ontogeny and overall ontogeny.

Our paper focuses on sensitive periods beyond early ontogeny, including (but not limited to) adolescence. Typically, adolescence corresponds to the life stage in which individuals experience physiological changes of puberty, paving the way for adulthood (Reddy et al., 2022). Sometimes, it is defined as the transition towards independence from caregivers (Romeo et al., 2016). However, this definition does not readily apply to species with different life cycles and definitions vary even within research literatures on a single species. Nonetheless, a transitory phase from juveniles to adults appears to be common across many species. For example, in species undergoing metamorphosis, researchers have drawn parallels between puberty and metamorphosis as the physiological process by which juveniles turn into adults (Barredo et al., 2021). For several of our empirical examples, 'adolescence' as a transitory phase provides a useful context for interpreting our findings.

3 | THREE EXPLANATIONS FOR SENSITIVE PERIODS BEYOND EARLY ONTOGENY

Across the four models, we extracted three different explanations for sensitive periods beyond early ontogeny: (1) increasing uncertainty about the environment, (2) increasing informativeness of cues, and (3) frequent changes in the environmental state (Figure 1). We will showcase these explanations and illustrate each one using empirical examples from various species (Table 1). We also discuss how the patterns of plasticity observed in theoretical and empirical research depend on the study protocols used to quantify plasticity.

3.1 | Explanation 1: Sensitive periods occur in mid-ontogeny when uncertainty increases over ontogeny

Three of the four models—Fischer et al. (2014), Stamps and Krishnan (2017), and Walasek et al. (2022b)—produce sensitive periods mid-ontogeny because uncertainty increases early in ontogeny (Figure 1, panel a). However, the causes of this increase in

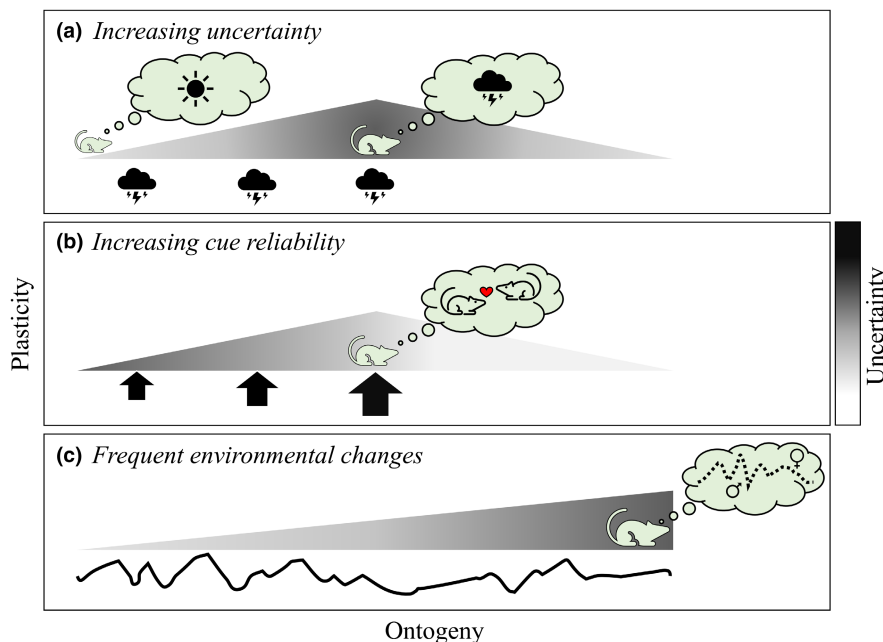


FIGURE 1 Plasticity tracks uncertainty across ontogeny. The height of the triangles indicates the level of plasticity; its shading the level of uncertainty; with darker shades indicating more uncertainty. Panel (a) shows that sensitive periods can occur mid-ontogeny if organisms become more uncertain about their phenotype-environment fit across early ontogeny. For example, rodents may have evolved to expect a safe environment (sun) and become more uncertain when they sample contradicting cues (thunder). Panel (b) shows that sensitive periods can also occur mid-ontogeny when cues (upward pointing arrows) become more reliable towards that time period, enabling organisms to reduce their uncertainty; with larger arrows indicating higher cue reliability. As an example, rodents might sample reliable cues from peers about their mate value. Panel (c) illustrates that sensitive periods towards the end of ontogeny can occur if changing environmental conditions (black, jiggly line) induce uncertainty about the adult environment. In such conditions, organisms might rely on the most recent information at the end of ontogeny to reduce their uncertainty and adjust their phenotypes. For example, rodents may exhibit heightened plasticity for social behaviours near adulthood because the population's sex ratio changes within their lifetimes.

uncertainty differ between these models. We will provide general insights in the main text and offer details in Box S1.

Fischer et al. (2014) assume a fluctuating environment in which the entire population starts ontogeny with an already induced phenotype. This phenotype reflects the inherited, long-term estimate of the environment ('evolutionary prior'). Crucially (and unlike in the other three models in our synthesis), adjusting this initial phenotype is assumed to be costly. Therefore, when cues are noisy, most organisms sample a few cues before adjusting their phenotype. When the environmental state changes slowly (relative to generation time), organisms become more uncertain about their current phenotype-environment match as they start to sample cues that contradict their priors. This results in sensitive periods early in ontogeny, but not at the onset (Figure 2, column 3, row 1 and 2, dark teal lines). When cues are low in reliability, it takes organisms longer to reach

sufficient confidence to make costly phenotypic adjustments, and some individuals never do. Averaged across the population, this results in later and lower peaks in plasticity (row 1). Rapidly changing environments within generations (light teal line) amplify this effect because phenotypic adjustments are potentially only useful for a short amount of time, resulting in even lower, mid-ontogeny peaks in plasticity.

In Walasek et al. (2022b), sensitive periods towards mid-ontogeny also occur due to mismatches between early ontogeny cues and priors, when the environment changes slowly within generations (Figure 2, column 3, solid red lines). Early in ontogeny, all organisms start specializing towards the long-term environment indicated by the prior. Plasticity increases when some organisms sample cues that contradict their early estimates and thus increase uncertainty about the current fit with the expected future environment. Averaged

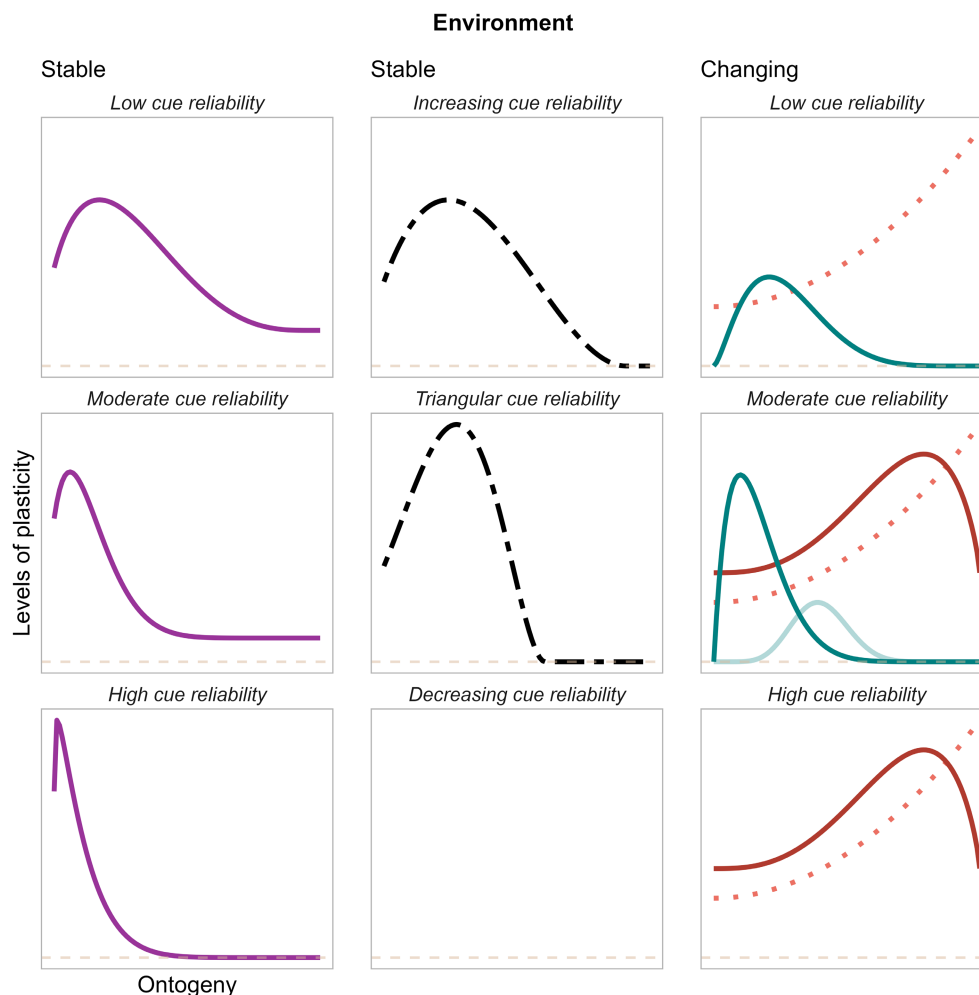


FIGURE 2 Explanations for sensitive periods beyond early ontogeny across models. Rows depict the level (low, moderate, high) or pattern (increasing, triangular, decreasing) of cue reliability. Columns depict whether the environmental state is stable or might change within an individual's lifespan. Colours indicate the four models discussed in the paper: In purple, Stamps and Krishnan (2017); in black, Walasek et al. (2022a); in red, Walasek et al. (2022b); and in teal, Fischer et al. (2014). Line types indicate different ultimate-level explanations for sensitive periods: Solid indicates increases in uncertainty, double-dash indicates increases in cue reliability, and dotted indicates changing environments. Colour intensity indicates the rate of environmental change (only in the third column): Light indicates fast and dark indicates slow changes. The figure omits patterns of sensitive periods early in ontogeny. Note that all models compute changes in plasticity across ontogeny as an average across members of the population. Individuals within a population may deviate from this average pattern.

across members of the population, such conditions result in mid- to late-ontogeny peaks in plasticity, driven by a subset of individuals.

In Stamps and Krishnan (2017), the environment does not fluctuate across ontogeny. However, they explored scenarios in which organisms with priors indicating a dangerous environment, receive contradicting cues indicating a safe environment. Similar to Fischer et al. (2014) and Walasek et al. (2022b), these initial cues (which contradict organisms early estimates of the environment) increase uncertainty. When uncertainty is highest, subsequent cues have the most impact on development, resulting in peak-plasticity beyond the onset of ontogeny (Figure 2, first column). The lower the cue reliability, the noisier cues are and the longer it takes for estimates to shift, resulting in mid-ontogeny peaks in plasticity (Figure 2, column 1, first row).

A common denominator across these three models is that uncertainty arises from cues which are markedly different from organisms' priors (Figure 1, panel a). This process can be linked to the 'discrepancy rule' derived from Bayesian models of development (Stamps & Frankenhuis, 2016). The discrepancy rule states that the extent to which individuals are shaped by a cue depends on how different the cue is from their prior estimate. There is experimental support for this rule in fruit flies (Stamps et al., 2018). However, this work did not focus on sensitive periods; it explored the impact of a cue in a single time period, rather than changes in the impact of cues over multiple time periods.

3.1.1 | Empirical studies

Empirical evidence suggests that increases in uncertainty, particularly about the social environment, can result in sensitive periods mid-ontogeny (Table 1). At a proximate level, such increases in plasticity might be initiated by 'prediction errors', resulting from mismatches between the expected and actual sensory input (Courville et al., 2006; Galván, 2010; Scott & Frank, 2023). Such mismatches can occur when organisms experience novel or changing environmental conditions. For example, human adolescents, who were adopted as children from relatively harsh conditions into more supportive conditions, show greater potential for stress recalibration than non-adopted individuals do (Gunnar et al., 2019). Here, drastic environmental changes may lead the brain to reevaluate the current phenotype-environment fit, temporarily increasing plasticity in cortisol stress reactivity.

Increases in uncertainty can also shape behaviour. Recent experiments in humans have revealed an 'adolescent-emerging' increase in information sampling before making decisions (Ciranka & van den Bos, 2020; Ma et al., 2022; Niebaum et al., 2022). For example, adolescents gather more information about the trustworthiness of others compared to other age groups (Ma et al., 2022). Adolescents aged 13 to 15 years were a priori more uncertain compared to younger and older peers and more willing to tolerate this uncertainty, resulting in increased information sampling. Taken together, adolescents may be more uncertain about features of their social environment,

resulting in increased exploration and sensitivity towards social information (Giron et al., 2023). Moreover, this pattern appears to be specific to social information; with non-social information, tolerance for uncertainty and exploration continuously declines with age (Nussenbaum et al., 2023).

We have found two examples in non-human animals. As in humans, chimpanzees show heightened exploration and learning in adolescence, potentially due to increased uncertainty about novel social environments (Reddy et al., 2022). And so do fish: Amazon molly (*Poecilia formosa*) show increased behavioural plasticity during the first weeks of life (Ehlman, Scherer, Bierbach, Stärk, et al., 2023). This prey species might start out with a prior indicating a dangerous environment. However, when reared in benign tanks, they likely sample cues indicating a safe environment, thus initially becoming more uncertain about environmental conditions. We suspect there are other examples in non-human animals. We hope our synthesis will foster connections between such examples and theory on sensitive periods.

3.2 | Explanation 2: Sensitive periods occur in mid-ontogeny when the reliability of cues increases across ontogeny

Walasek et al. (2022a) explore changes in the reliability of cues across ontogeny in an environment that varies between generations, but remains stable within an individual's lifetime. The authors focus on three different patterns of change: increasing, first increasing and then decreasing ('triangular'), and decreasing cue reliabilities. They found sensitive periods in mid-ontogeny when the reliability of cues increases across some portion of ontogeny (Figure 2, column 2). When the reliability of cues decreases, sensitive periods only occur early in ontogeny. Under these conditions, cues at the onset of ontogeny are highly indicative of a stable ontogenetic environment, so there is no need for organisms to maintain high levels of plasticity. The reliability of cues can vary for various reasons. For some traits, cues may only be available or more abundant during certain developmental stages, such as social cues about an individual's mate value (Fawcett & Frankenhuis, 2015). The higher the frequency of cues is, the more reliably organisms can use them to estimate their environment. Another reason could be that, through sensory development, organisms become better able to detect and use cues later in ontogeny. Relatedly, if neural systems age, an organism's ability to detect and accurately process cues may degrade, resulting in declining cue reliability.

3.2.1 | Empirical studies

We expect mid-ontogeny sensitive periods when reliable cues are more readily available in mid-ontogeny (Figure 1, panel b) and when sensory and neural systems are better prepared to process these cues (Dahl et al., 2018; Larsen & Luna, 2018). Empirical studies in humans and rodents support such an explanation (Table 1). This

work indicates the existence of sensitive periods for social behaviour in response to cues from peers and potential mates during adolescence (Cohodes et al., 2023; Hofmans & van den Bos, 2022; Li et al., 2021; Sachser et al., 2018). For example, human adolescents show heightened susceptibility to feedback from peers (Hofmans & van den Bos, 2022; Molleman et al., 2022). In rodents, social defeat and isolation during adolescence have long-lasting effects on social behaviours, such as aggression, exploration, and play (Li et al., 2021; Sachser et al., 2018). At an ultimate level, adolescence may be particularly important for social behaviours due to the availability of novel social landscapes. At a proximate level, neural restructuring and hormonal changes during adolescence facilitate learning about these social landscapes.

In mammals, adolescence marks a novel life stage of independence and exposure to peers (Buwalda et al., 2011). For the first time, organisms can sample cues that are not influenced by their parents or caregivers (Bebbington & Groothuis, 2021; Del Giudice, 2012; Sachser et al., 2018). This is important as parents have their own interests in mind and may provide suboptimal cues to their offspring. This conflict arises because parents only share 50% of their genes with their offspring and an offspring shares 100% of their genes with themselves (i.e. parent-offspring conflict; Godfray, 1995; Trivers, 1974). Thus, what is best for the parent may not always be best for the offspring. Such parent-offspring conflict is especially prevalent in species with prolonged postnatal care, such as humans or other long-lived mammals (Del Giudice, 2012). The longer children receive cues from their parents, the more parents can shape their offspring's developmental trajectories in their own interest. Thus, adolescence offers an opportunity to sample cues that are more aligned with the offspring's own interests and may, therefore, more reliably index their environment.

This influx of novel social experiences coincides with changes in brain structures relevant for social information processing (Hofmans & van den Bos, 2022; Raab & Hartley, 2019). One example of a neurophysiological system showing protracted development into adolescence is the dopamine system and its associated brain regions (Lin et al., 2020). The 'late' development of these brain regions, which are involved in learning and decision-making, may enable adolescent mammals to process the novel social environment they face.

Combining insights across explanations, mammalian brains may have evolved to be sensitive to both increasing uncertainty and increasing cue reliability during adolescence (Figure 1, panels a, b). At a proximate level, we have discussed neurophysiological changes and greater availability of novel experiences and opportunities as factors initiating sensitive periods. While both of these proximate factors play a role in shaping plasticity, their contributions might vary for different traits. One principled way in which these factors might interact is through 'metaplasticity', the adaptive control of plasticity (Frankenhuis & Gopnik, 2023; Scott & Frank, 2023; Soltani & Izquierdo, 2019). In line with metaplasticity, novel experiences and opportunities might modulate neurophysiological processes controlling levels of plasticity.

3.3 | Explanation 3: Sensitive periods occur late in ontogeny when the environment changes frequently

Walasek et al. (2022b) found that frequent environmental fluctuations within generations may favour sensitive periods at the end of ontogeny (Figure 1, panel c; Figure 2, column 3, dotted light red lines). This finding is unique compared with all other models of the evolution of sensitive periods. Notably, Fischer et al. (2014), who modelled environmental fluctuations in a similar manner as Walasek et al. (2022b), did not observe sensitive periods towards the end of ontogeny. However, unlike Fischer et al., Walasek et al. assume that fitness only accrues at the end of ontogeny (Box S1). This assumption might more likely apply to morphological traits than to behavioural traits, which might be more malleable throughout life. However, not all morphological traits become fixed at a specific age or life stage (Burggren, 2020) and not all behaviours are plastic throughout the entire lifespan (Bell et al., 2009). Walasek et al.'s (2022b) assumption can also apply to cases where behaviour remains plastic throughout the entire lifespan, when fitness effects are largest at a specific stage, such as the transition to adulthood. More generally, for traits that become fixed or accrue the largest fitness effects after maturation, organisms need to build phenotypes that match the long-term future environment. When the environment changes frequently, it makes sense to be most sensitive to cues towards the end of ontogeny as these cues are better predictors of the future environment (Tariel-Adam et al., 2023; Figure 1, panel c).

3.3.1 | Empirical studies

There are fewer empirical examples of sensitive periods towards the end of ontogeny than there are examples of sensitive periods in mid- or early ontogeny. It is an open question to what extent this asymmetry reflects the natural world or merely the focus of research (e.g. on particular species). In fact, although most of the examples we have discussed so far feature vertebrates, especially primates and rodents, there are clear examples of sensitive periods late in ontogeny in a range of invertebrates, including mites, water fleas, and wasps (Table 1), described below.

Consider morph development in male bulb mites (*Rhizoglyphus robini*). Whether males mature into bigger fighters or defenceless scramblers strongly depends on their size during the final developmental stage (3rd instar) (Smallegange, 2011). Their size at this stage depends on nutritional conditions across ontogeny, with richer foods resulting in larger size. When bulb mites temporarily experience lower-quality food during the protonymph stage, they cannot compensate for lost growth if given richer foods during the final instar stage (Leigh & Smallegange, 2014). Thus, we may hypothesize that body size at the end of ontogeny summarizes environmental conditions across ontogeny and helps predict future environmental conditions, favouring a late sensitive period for male morph development.

Another example involves female water fleas (*Daphnia magna*) being exposed to predation threat during the developmental stage

prior to reproduction (4th instar) (Mikulski & Pijanowska, 2010). These females develop to be much smaller at maturity than females who experienced threat at earlier instar stages or no threat at any instar stage. Notably, these effects carried over to their daughters. Compared to controls, daughters of mothers exposed to predators late in ontogeny showed the largest reduction in their size at maturity as well as in their number of offspring. A potential explanation for such a late sensitive period could be that experiences of threat close to the onset of reproduction indicate a high chance of predation at maturity. Thus, a late-ontogeny sensitive period conveys a fitness benefit: Responding to imminent threat with a smaller size at first reproduction makes it more likely for mothers to release her offspring before being eaten.

Sensitive periods in early adulthood also occur for social behaviours. Recent work in paper wasps (*Polistes dominula*) shows that nest-mate recognition is shaped primarily by the adult social environment (i.e. colony composition) and not genetic predisposition or early experiences, as previously thought (Cappa et al., 2020). In rodents, the evidence for sensitive periods in social behaviours late in ontogeny is less clear. Although rodents may preserve heightened plasticity in adulthood to adapt to changing social conditions (MacLeod et al., 2023; Mutwill et al., 2020), it is not clear whether this heightened plasticity exceeds levels of plasticity during adolescence. That changing environmental conditions can retain plasticity late in ontogeny has been empirically documented across various species and traits (Kotrschal & Taborsky, 2010; Relyea, 2003). This association between changing environmental conditions and (heightened or persisting) late-ontogeny plasticity might be mediated through an increase in neurons (i.e. neurogenesis) from exposure to diverse environments (enrichment) (Freund et al., 2013, 2015; Kempermann et al., 2002; Lefevre et al., 2023; Sherry & Hoshoooley, 2010).

4 | WHY DO SENSITIVE PERIODS EMERGE BEYOND EARLY ONTOGENY?

Across models, sensitive periods beyond early ontogeny appear to be driven by changes in uncertainty. Sensitive periods emerge towards the middle or end of ontogeny when an organism's uncertainty about the environment-phenotype fit increases later in ontogeny (Figure 1, panels a, c). Sensitive periods may also occur mid-ontogeny when cues later in ontogeny reduce uncertainty more than earlier cues do (Figure 1, panel b).

Across empirical examples, an interesting possibility is that sensitive periods later in ontogeny tend to occur in species that undergo metamorphosis, such as mites, water fleas, and wasps. Across developmental stages, these species typically experience drastic changes in sensory physiology and mobility (English & Barreaux, 2020). Thus, it is conceivable that organisms' ability to sense cues may increase across ontogeny or that organisms can only access cues at certain ontogenetic stages. Additionally, increases in mobility of some morphs (e.g. through the development of wings) allow organisms to experience novel and changing environmental

conditions. We do not know of studies that report sensitive periods later in ontogeny due to changes in the reliability of cues or in the environmental state following morphological reorganization. It is possible that researchers might study a species that only responds to a particular cue in later stages of metamorphosis, without describing such a response as a 'sensitive period later in ontogeny'. Instead, they may merely refer to it as plasticity. We see scope for future work to review sensitive periods in (in)vertebrate systems focusing on late stages of metamorphosis. In the discussion section, we highlight modelling directions that can strengthen the theoretical foundation for such work.

Lastly, we note that the same model or experiment could lead to different conclusions about the timing of plasticity depending on the study protocol (Stamps & Luttbeg, 2022; Walasek et al., 2022a). Understanding the role of the study protocol is thus important for interpreting and comparing results from different mathematical models, and for linking empirical findings. We elaborate on the role of study protocol in Boxes S2 and S3.

5 | SENSITIVE PERIODS BEYOND EARLY ONTOGENY: INSIGHTS AND GAPS

Our synthesis offers three main insights. First, models suggest that natural selection favours levels of plasticity to track changes in organisms' uncertainty and the potential of cues to reduce it. Second, our selection of models and empirical examples includes more cases of sensitive periods mid-ontogeny than towards the end of ontogeny. Third, most examples of sensitive periods beyond early ontogeny involve social behaviour in mammals. At present, we do not know whether sensitive periods in mid-ontogeny are more common in mammals, or have merely received more attention from researchers than other life stages, species, and traits. Systematic reviews and meta-analyses can distinguish between these possibilities.

We have also identified two gaps. First, there are few empirical studies specifically designed to test predictions from sensitive period models. Second, only a handful of models have explored sensitive periods later in ontogeny and these models do not incorporate recent empirical findings. Below, we suggest four different types of future directions to address these gaps, thus strengthening connections between theoretical and empirical studies.

First, although many empirical studies examine plasticity in response to cues during a specific ontogenetic stage, only a few studies consider multiple time periods. To delineate the timing and duration of sensitive periods, we need experiments that cover multiple ontogenetic stages. Ideally, researchers would have access to near-continuous measures across ontogeny. Recent advancements in animal tracking and the ability to collect and process large amounts of data bring us closer to this ideal scenario (Dupont et al., 2024; Ehman, Scherer, Bierbach, Francisco, et al., 2023; Kievit et al., 2021). Earlier, we featured a study of the Amazon molly (*P. formosa*) illustrating the potential

of these advancements: Using high-resolution tracking tanks, the researchers measured behavioural plasticity on a nearly continuous basis across ontogeny (Ehlman, Scherer, Bierbach, Stärk, et al., 2023). Extending such experiments to cover multiple generations can additionally provide answers to questions about sensitive periods for transgenerational plasticity (Tariel-Adam et al., 2023). That is, during which ontogenetic windows do parents' experiences induce phenotypic changes in the next generation?

A second important future direction is to experimentally test model predictions about the evolution of sensitive periods later in ontogeny. Experimental evolution offers unique opportunities in this area. This approach typically uses species with a short generation time to study how controlled manipulation of the environment (e.g. cues) shapes evolution. For example, experimental evolution studies in fruit flies (*Drosophila melanogaster*) have been successfully used to test theories about learning (Mery & Kawecki, 2002). This work has, for example, illustrated the necessary environmental conditions for learning to evolve (Dunlap & Stephens, 2014). Fruit flies evolve to learn the best site for oviposition in predictably changing environments but not in stable environments with unreliable cues. The authors have also demonstrated conditions for the evolution of 'prepared learning' (Dunlap & Stephens, 2014). Prepared learning allows organisms to more easily learn some stimulus-consequence associations (e.g. association between odour and fitness benefits of an oviposition site) than others. In the experiment, fruit flies evolve prepared learning only when cues reliably predict stimulus-consequence associations across evolutionary time scales. We currently lack similar studies that manipulate experiences across multiple time periods to test predictions about sensitive periods. Insect and invertebrate model systems are particularly well-suited to reducing the gap between theoretical predictions and empirical insights about sensitive periods (English & Barreaux, 2020).

Third, to increase synergies between theory and empirical research, future models could do more to incorporate existing empirical findings (see Metcalf et al., 2022 for an exemplary model exploring the evolution of immune system tolerance). The models reviewed here tend to be agnostic about the type of experience organisms face (e.g. positive vs. negative) and the specific trait they develop (e.g. a defence against predators or a specific social trait). Future work can extend existing evolutionary models by explicitly implementing novel empirical findings about specific traits or classes of traits (e.g. social behaviours) (Frankenhuis et al., 2018; Kacelnik, 2012; McNamara & Houston, 2009). For example, we could incorporate recent findings about sensitive periods for social traits into an existing model of the evolution of helping behaviours (Kuijper & Johnstone, 2019). This model explored the development of helping behaviours only in response to early-life social adversity. An extension of this work could explore plasticity in response to social experiences (both negative and positive) later in ontogeny as well. Generally, there are few models exploring the evolution of sensitive periods beyond early ontogeny in the context of social

dynamics. By incorporating social interactions among individuals, including frequency-dependent selection, future models can shed light on the role of the social environment in favouring mid-ontogeny sensitive periods.

Lastly, models of sensitive period evolution can be tailored towards specific species and traits by considering their life histories. We see at least three exciting directions for future modelling. First, models can explicitly incorporate transitions between different life stages (such as metamorphosis) to capture a broader variety of species. For example, such models can study how cues received as larvae can shape their development as adults with increased mobility and sensory capacity (English & Barreaux, 2020). These models could also explore whether experiencing changing environmental conditions or more reliable cues in later stages of metamorphosis induces heightened plasticity. Second, models can vary fitness benefits across ontogeny (Mangel & Clark, 1988). In many species survival and fertility are likely more strongly shaped during some life stages than others. For example, it is possible that adjusting morphologies shortly before maturation could increase survival and reproduction (e.g. as seen in Mikulski & Pijanowska, 2010). Similarly, tailoring social behaviours to the adolescent social environment likely influences future reproductive success (Sachser et al., 2020). A formal investigation of these ideas is currently lacking. Third, models of sensitive periods to date have barely explored life-history trade-offs. Yet, several of the empirical patterns in Table 1 could well reflect trade-offs between fertility and survival. Life-history trade-offs might for example be involved in shaping the different male morphs (fighters vs. scramblers) in bulb mites (*R. robini*) (Deere & Smallegange, 2023; Smallegange et al., 2019). In poor environmental conditions, benign scramblers may be at an advantage for they can reach sexual maturity faster than fighters. How exactly these trade-offs shape male morph development is not yet understood. Future models could embed such trade-offs, for example, by allowing individuals to choose when to terminate ontogeny for a specific trait and/or transition (or metamorphose) into the next developmental stage (Relyea, 2007).

Moving forward, stronger connections between carefully designed empirical studies and models can provide a more organized approach to studying sensitive periods. Ultimately, synergies between theoretical and empirical work, and clear connections between proximate and ultimate explanations, can promote an integrative science of sensitive periods.

AUTHOR CONTRIBUTIONS

NW and WEF conceived and developed the ideas in this paper. NW conducted the synthesis of mathematical models and empirical papers and wrote the first draft. NW, WEF, and KP revised the draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were collected or used for this paper.

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REFERENCES

- Barredo, C. G., Gil-Martí, B., Deveci, D., Romero, N. M., & Martin, F. A. (2021). Timing the juvenile-adult neurohormonal transition: Functions and evolution. *Frontiers in Endocrinology*, 11, 602285. <https://doi.org/10.3389/fendo.2020.602285>
- Bateson, P., & Laland, K. N. (2013). Tinbergen's four questions: An appreciation and an update. *Trends in Ecology & Evolution*, 28(12), 712–718. <https://doi.org/10.1016/j.tree.2013.09.013>
- Bebbington, K., & Groothuis, T. G. G. (2021). Who listens to mother? A whole-family perspective on the evolution of maternal hormone allocation. *Biological Reviews*, 4, 1951–1968. <https://doi.org/10.1111/brv.12733>
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, 77(4), 771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Bergman, T. J., & Beehner, J. C. (2022). Leveling with Tinbergen: Four levels simplified to causes and consequences. *Evolutionary Anthropology: Issues, News, and Reviews*, 31(1), 12–19. <https://doi.org/10.1002/evan.21931>
- Botero, C. A., Weissing, F. J., Wright, J., & Rubenstein, D. R. (2015). Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences of the United States of America*, 112(1), 184–189. <https://doi.org/10.1073/pnas.1408589111>
- Burggren, W. W. (2020). Phenotypic switching resulting from developmental plasticity: Fixed or reversible? *Frontiers in Physiology*, 10(January), 1–13. <https://doi.org/10.3389/fphys.2019.01634>
- Buwalda, B., Geerdink, M., Vidal, J., & Koolhaas, J. M. (2011). Social behavior and social stress in adolescence: A focus on animal models. *Neuroscience & Biobehavioral Reviews*, 35(8), 1713–1721. <https://doi.org/10.1016/j.neubiorev.2010.10.004>
- Cappa, F., Cini, A., Signorotti, L., & Cervo, R. (2020). Rethinking recognition: Social context in adult life rather than early experience shapes recognition in a social wasp. *Philosophical Transactions of the Royal Society B*, 375(1802), 20190468. <https://doi.org/10.1098/rstb.2019.0468>
- Ciranka, S., & van den Bos, W. (2020). A Bayesian model of social influence under risk and uncertainty. *PsyArXiv*. <https://doi.org/10.31234/osf.io/mujek>
- Cohodes, E. M., Sisk, L. M., Keding, T. J., Mandell, J. D., Notti, M. E., & Gee, D. G. (2023). Characterizing experiential elements of early-life stress to inform resilience: Buffering effects of controllability and predictability and the importance of their timing. *Development and Psychopathology*, 35(5), 2288–2301. <https://doi.org/10.1017/S0954579423000822>
- Courville, A. C., Daw, N. D., & Touretzky, D. S. (2006). Bayesian theories of conditioning in a changing world. *Trends in Cognitive Sciences*, 10(7), 294–300. <https://doi.org/10.1016/j.tics.2006.05.004>
- Dahl, R. E., Allen, N. B., Wilbrecht, L., & Suleiman, A. B. (2018). Importance of investing in adolescence from a developmental science perspective. *Nature*, 554(7693), 441–450. <https://doi.org/10.1038/nature25770>
- Deere, J. A., & Smallegange, I. M. (2023). Individual differences in developmental trajectory leave a male polyphenic signature in bulb mite populations. *Peer Community Journal*, 3, e117. <https://doi.org/10.24072/pcjournal.351>
- Del Giudice, M. (2012). Fetal programming by maternal stress: Insights from a conflict perspective. *Psychoneuroendocrinology*, 37(10), 1614–1629. <https://doi.org/10.1016/j.psyneuen.2012.05.014>
- DePasquale, C. E., Herzberg, M. P., & Gunnar, M. R. (2021). The pubertal stress recalibration hypothesis: Potential neural and behavioral consequences. *Child Development Perspectives*, 15(4), 249–256. <https://doi.org/10.1111/cdep.12429>
- Dunlap, A. S., & Stephens, D. W. (2014). Experimental evolution of prepared learning. *PNAS*, 111(32), 11750–11755. <https://doi.org/10.1073/pnas.1404176111>
- Dupont, L., Thierry, M., Zinger, L., Legrand, D., & Jacob, S. (2024). Beyond reaction norms: The temporal dynamics of phenotypic plasticity. *Trends in Ecology & Evolution*, 39(1), 41–51. <https://doi.org/10.1016/j.tree.2023.08.014>
- Ehlman, S. M., Scherer, U., Bierbach, D., Francisco, F. A., Laskowski, K. L., Krause, J., & Wolf, M. (2023). Leveraging big data to uncover the eco-evolutionary factors shaping behavioural development. *Proceedings of the Royal Society B*, 290(1992), 20222115. <https://doi.org/10.1098/rspb.2022.2115>
- Ehlman, S. M., Scherer, U., Bierbach, D., Stärk, L., Beese, M., & Wolf, M. (2023). Developmental arcs of plasticity in whole movement repertoires of a clonal fish. *bioRxiv*. <https://doi.org/10.1101/2023.12.07.570540>
- English, S., & Barreaux, A. M. (2020). The evolution of sensitive periods in development: Insights from insects. *Current Opinion in Behavioral Sciences*, 36, 71–78. <https://doi.org/10.1016/j.cobeha.2020.07.009>
- Eriksson, M., Nylin, S., & Carlsson, M. A. (2019). Insect brain plasticity: Effects of olfactory input on neuropil size. *Royal Society Open Science*, 6(8), 190875. <https://doi.org/10.1098/rsos.190875>
- Fawcett, T. W., & Frankenhuis, W. E. (2015). Adaptive explanations for sensitive windows in development. *Frontiers in Zoology*, 12(Suppl. 1), S3. <https://doi.org/10.1186/1742-9994-12-S1-S3>
- Fischer, B., van Doorn, G. S., Dieckmann, U., & Taborsky, B. (2014). The evolution of age-dependent plasticity. *The American Naturalist*, 183(1), 108–125. <https://doi.org/10.1086/674008>
- Frankenhuis, W. E., & Fraley, R. C. (2017). What do evolutionary models teach us about sensitive periods in psychological development? *European Psychologist*, 22(3), 141–150. <https://doi.org/10.1027/1016-9040/a000265>
- Frankenhuis, W. E., & Gopnik, A. (2023). Early adversity and the development of explore–exploit tradeoffs. *Trends in Cognitive Sciences*, 27(7), 616–630. <https://doi.org/10.1016/j.tics.2023.04.001>
- Frankenhuis, W. E., & Panchanathan, K. (2011). Balancing sampling and specialization: An adaptationist model of incremental development. *Proceedings of the Royal Society B*, 278(1724), 3558–3565. <https://doi.org/10.1098/rspb.2011.0055>
- Frankenhuis, W. E., Panchanathan, K., & Barto, A. G. (2018). Enriching behavioral ecology with reinforcement learning methods. *Behavioural Processes*, 161, 94–100. <https://doi.org/10.1016/j.beproc.2018.01.008>
- Frankenhuis, W. E., & Walasek, N. (2020). Modeling the evolution of sensitive periods. *Developmental Cognitive Neuroscience*, 41(November 2019), 100715. <https://doi.org/10.1016/j.dcn.2019.100715>
- Freund, J., Brandmaier, A. M., Lewejohann, L., Kirste, I., Kritzler, M., Kruger, A., Sachser, N., Lindenberger, U., & Kempermann, G. (2013). Emergence of individuality in genetically identical mice. *Science*, 340(6133), 756–759. <https://doi.org/10.1126/science.1235294>

- Freund, J., Brandmaier, A. M., Lewejohann, L., Kirste, I., Kritzler, M., Krüger, A., Sachser, N., Lindenberger, U., & Kempermann, G. (2015). Association between exploratory activity and social individuality in genetically identical mice living in the same enriched environment. *Neuroscience*, 309, 140–152. <https://doi.org/10.1016/j.neurosci.2015.05.027>
- Fuchs, E., & Flügge, G. (2014). Adult neuroplasticity: More than 40 years of research. *Neural Plasticity*, 2014, 541870. <https://doi.org/10.1155/2014/541870>
- Fuhrmann, D., Knoll, L. J., & Blakemore, S. J. (2015). Adolescence as a sensitive period of brain development. *Trends in Cognitive Sciences*, 19(10), 558–566. <https://doi.org/10.1016/j.tics.2015.07.008>
- Gabard-Durnam, L., & McLaughlin, K. A. (2020). Sensitive periods in human development: Charting a course for the future. *Current Opinion in Behavioral Sciences*, 36, 120–128. <https://doi.org/10.1016/j.cobeha.2020.09.003>
- Gabriel, W. (2006). Selective advantage of irreversible and reversible phenotypic plasticity. *Archiv für Hydrobiologie*, 167(1–2), 1–20.
- Galván, A. (2010). Neural plasticity of development and learning. *Human Brain Mapping*, 31(6), 879–890. <https://doi.org/10.1002/hbm.21029>
- Ganz, J., & Brand, M. (2016). Adult neurogenesis in fish. *Cold Spring Harbor Perspectives in Biology*, 8(7), a019018. <https://doi.org/10.1101/cshperspect.a019018>
- Giron, A. P., Ciranka, S., Schulz, E., van den Bos, W., Ruggeri, A., Meder, B., & Wu, C. M. (2023). Developmental changes in exploration resemble stochastic optimization. *Nature Human Behaviour*, 7(11), 1955–1967. <https://doi.org/10.1038/s41562-023-01662-1>
- Godfray, H. C. J. (1995). Evolutionary theory of parent–offspring conflict. *Nature*, 376(6536), 133–138. <https://doi.org/10.1038/376133a0>
- Gunnar, M. R., DePasquale, C. E., Reid, B. M., Donzella, B., & Miller, B. S. (2019). Pubertal stress recalibration reverses the effects of early life stress in postinstitutionalized children. *Proceedings of the National Academy of Sciences of the United States of America*, 116(48), 23984–23988. <https://doi.org/10.1073/pnas.1909699116>
- Hofmans, L., & van den Bos, W. (2022). Social learning across adolescence: A Bayesian neurocognitive perspective. *Developmental Cognitive Neuroscience*, 58, 101151. <https://doi.org/10.1016/j.dcn.2022.101151>
- Kacelnik, A. (2012). Putting mechanisms into behavioral ecology. In P. Hammerstein & R. Stevens (Eds.), *Evolution and the mechanisms of decision making* (pp. 21–38). MIT Press.
- Kempermann, G., Gast, D., & Gage, F. H. (2002). Neuroplasticity in old age: Sustained fivefold induction of hippocampal neurogenesis by long-term environmental enrichment. *Annals of Neurology*, 52(2), 135–143. <https://doi.org/10.1002/ana.10262>
- Kievit, R. A., McCormick, E. M., Fuhrmann, D., Deserno, M. K., & Orben, A. (2021). Using large, publicly available datasets to study adolescent development: Opportunities and challenges. *Current Opinion in Psychology*, 44, 303–308. <https://doi.org/10.1016/j.copsyc.2021.10.003>
- Knudsen, E. I. (2004). Sensitive periods in the development of the brain and behavior. *Journal of Cognitive Neuroscience*, 16(8), 1412–1425. <https://doi.org/10.1162/08998929042304796>
- Kotrschal, A., & Taborsky, B. (2010). Environmental change enhances cognitive abilities in fish. *PLoS Biology*, 8(4), e1000351. <https://doi.org/10.1371/journal.pbio.1000351>
- Kuijper, B., & Johnstone, R. A. (2019). The evolution of early-life effects on social behaviour—Why should social adversity carry over to the future? *Philosophical Transactions of the Royal Society B*, 374(1770), 1–18. <https://doi.org/10.1098/rstb.2018.0111>
- Larsen, B., & Luna, B. (2018). Adolescence as a neurobiological critical period for the development of higher-order cognition. *Neuroscience & Biobehavioral Reviews*, 94, 179–195. <https://doi.org/10.1016/j.neubiorev.2018.09.005>
- Lefevre, M., Lu, C., Botero, C. A., & Rutkowska, J. (2023). Variable ambient temperature promotes song learning and production in zebra finches. *Behavioral Ecology*, 34(3), 408–417. <https://doi.org/10.1093/beheco/ara014>
- Leigh, D. M., & Smallegange, I. M. (2014). Effects of variation in nutrition on male morph development in the bulb mite *Rhizoglyphus robini*. *Experimental and Applied Acarology*, 64(2), 159–170. <https://doi.org/10.1007/s10493-014-9822-y>
- Li, D. C., Hinton, E. A., & Gourley, S. L. (2021). Persistent behavioral and neurobiological consequences of social isolation during adolescence. *Seminars in Cell & Developmental Biology*, 118, 73–82. <https://doi.org/10.1016/j.semcd.2021.05.017>
- Lin, W. C., Delevich, K., & Wilbrecht, L. (2020). A role for adaptive developmental plasticity in learning and decision making. *Current Opinion in Behavioral Sciences*, 36, 48–54. <https://doi.org/10.1016/j.cobeha.2020.07.010>
- Ma, I., Westhoff, B., & van Duijvenvoorde, A. C. K. (2022). Uncertainty about others' trustworthiness increases during adolescence and guides social information sampling. *Scientific Reports*, 12(1), 7634. <https://doi.org/10.1038/s41598-022-09477-2>
- MacLeod, K. J., English, S., Ruuskanen, S. K., & Taborsky, B. (2023). Stress in the social context: A behavioural and eco-evolutionary perspective. *Journal of Experimental Biology*, 226(15), jeb245829. <https://doi.org/10.1242/jeb.245829>
- Mangel, M., & Clark, C. W. (1988). *Dynamic modeling in behavioral ecology* (Vol. 8). Princeton University Press.
- McNamara, J. M., & Houston, A. I. (2009). Integrating function and mechanism. *Trends in Ecology & Evolution*, 24(12), 670–675. <https://doi.org/10.1016/j.tree.2009.05.011>
- Mery, F., & Kawecki, T. J. (2002). Experimental evolution of learning ability in fruit flies. *Proceedings of the National Academy of Sciences of the United States of America*, 99(22), 14274–14279. <https://doi.org/10.1073/pnas.222371199>
- Metcalfe, C. J. E., Tepekule, B., Bruijning, M., & Koskella, B. (2022). Hosts, microbiomes, and the evolution of critical windows. *Evolution Letters*, 6(6), 412–425. <https://doi.org/10.1002/evl3.298>
- Mikulski, A., & Pijanowska, J. (2010). When and how can *Daphnia* prepare their offspring for the threat of predation? *Hydrobiologia*, 643(1), 21–26. <https://doi.org/10.1007/s10750-010-0131-0>
- Molleman, L., Ciranka, S., & van Den Bos, W. (2022). Social influence in adolescence as a double-edged sword. *Proceedings of the Royal Society B*, 289(1977), 20220045. <https://doi.org/10.1098/rspb.2022.0045>
- Mutwill, A. M., Zimmermann, T. D., Hennicke, A., Richter, S. H., Kaiser, S., & Sachser, N. (2020). Adaptive reshaping of the hormonal phenotype after social niche transition in adulthood. *Proceedings of the Royal Society B*, 287(1928), 20200667. <https://doi.org/10.1098/rspb.2020.0667>
- Mutwill, A. M., Zimmermann, T. D., Reuland, C., Fuchs, S., Kunert, J., Richter, S. H., Kaiser, S., & Sachser, N. (2019). High reproductive success despite queuing—Socio-sexual development of males in a complex social environment. *Frontiers in Psychology*, 10, 2810. <https://doi.org/10.3389/fpsyg.2019.02810>
- Niebaum, J. C., Kramer, A.-W., Huizenga, H. M., & van den Bos, W. (2022). Adolescents sample more information prior to decisions than adults when effort costs increase. *Developmental Psychology*, 58(10), 1974–1985. <https://doi.org/10.1037/dev0001397>
- Nussenbaum, K., Martin, R. E., Maulhardt, S., Yang, Y., Bizzell-Hatcher, G., Bhatt, N. S., Koenig, M., Rosenbaum, G. M., O'Doherty, J. P., Cockburn, J., & Hartley, C. A. (2023). Novelty and uncertainty differentially drive exploration across development. *eLife*, 12, e84260. <https://doi.org/10.7554/eLife.84260>
- Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, 18(5), 228–233. [https://doi.org/10.1016/S0169-5347\(03\)00036-3](https://doi.org/10.1016/S0169-5347(03)00036-3)
- Powers, A. S. (2016). Plasticity and adult neurogenesis in amphibians and reptiles: More questions than answers. *Brain, Behavior and Evolution*, 87(3), 175–183. <https://doi.org/10.1159/000447047>

- Raab, H., & Hartley, C. (2019). Adolescents exhibit reduced Pavlovian biases on instrumental learning. *Scientific Reports*, 10, 15770. <https://doi.org/10.31234/osf.io/38vgr>
- Reddy, R. B., Sandel, A. A., & Dahl, R. E. (2022). Puberty initiates a unique stage of social learning and development prior to adulthood: Insights from studies of adolescence in wild chimpanzees. *Developmental Cognitive Neuroscience*, 58, 101176. <https://doi.org/10.1016/j.dcn.2022.101176>
- Relyea, R. A. (2003). Predators come and predators go: The reversibility of predator-induced traits. *Ecology*, 84(7), 1840–1848. [https://doi.org/10.1890/0012-9658\(2003\)084\[1840:PCAPGT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1840:PCAPGT]2.0.CO;2)
- Relyea, R. A. (2007). Getting out alive: How predators affect the decision to metamorphose. *Oecologia*, 152(3), 389–400. <https://doi.org/10.1007/s00442-007-0675-5>
- Romeo, R. D., Patel, R., Pham, L., & So, V. M. (2016). Adolescence and the ontogeny of the hormonal stress response in male and female rats and mice. *Neuroscience & Biobehavioral Reviews*, 70, 206–216. <https://doi.org/10.1016/j.neubiorev.2016.05.020>
- Rundle, S. D., & Spicer, J. I. (2016). Heterokairy: A significant form of developmental plasticity? *Biology Letters*, 12(9), 20160509. <https://doi.org/10.1098/rsbl.2016.0509>
- Sachser, N., Hennessy, M. B., & Kaiser, S. (2018). The adaptive shaping of social behavioural phenotypes during adolescence. *Biology Letters*, 14(11), 20180536. <https://doi.org/10.1098/rsbl.2018.0536>
- Sachser, N., Zimmermann, T. D., Hennessy, M. B., & Kaiser, S. (2020). Sensitive phases in the development of rodent social behavior. *Current Opinion in Behavioral Sciences*, 36, 63–70. <https://doi.org/10.1016/j.cobeha.2020.07.014>
- Scott, D. N., & Frank, M. J. (2023). Adaptive control of synaptic plasticity integrates micro- and macroscopic network function. *Neuropsychopharmacology*, 48(1), 121–144. <https://doi.org/10.1038/s41386-022-01374-6>
- Sherry, D. F., & Hoshoooley, J. S. (2010). Seasonal hippocampal plasticity in food-storing birds. *Philosophical Transactions of the Royal Society B*, 365(1542), 933–943. <https://doi.org/10.1098/rstb.2009.0220>
- Smallegange, I. M. (2011). Complex environmental effects on the expression of alternative reproductive phenotypes in the bulb mite. *Evolutionary Ecology*, 25(4), 857–873. <https://doi.org/10.1007/s10682-010-9446-6>
- Smallegange, I. M., Rhebergen, F. T., & Stewart, K. A. (2019). Cross-level considerations for explaining selection pressures and the maintenance of genetic variation in condition-dependent male morphs. *Current Opinion in Insect Science*, 36, 66–73. <https://doi.org/10.1016/j.cois.2019.08.005>
- Snell-Rood, E. C., & Steck, M. K. (2019). Behaviour shapes environmental variation and selection on learning and plasticity: Review of mechanisms and implications. *Animal Behaviour*, 147, 147–156. <https://doi.org/10.1016/j.anbehav.2018.08.007>
- Soltani, A., & Izquierdo, A. (2019). Adaptive learning under expected and unexpected uncertainty. *Nature Reviews Neuroscience*, 20(10), 635–644. <https://doi.org/10.1038/s41583-019-0180-y>
- Stamps, J. A., Biro, P. A., Mitchell, D. J., & Saltz, J. B. (2018). Bayesian updating during development predicts genotypic differences in plasticity. *Evolution*, 72(10), 2167–2180. <https://doi.org/10.1111/evo.13585>
- Stamps, J. A., & Frankenhuis, W. E. (2016). Bayesian models of development. *Trends in Ecology & Evolution*, 31(4), 260–268. <https://doi.org/10.1016/j.tree.2016.01.012>
- Stamps, J. A., & Krishnan, V. V. (2017). Age-dependent changes in behavioural plasticity: Insights from Bayesian models of development. *Animal Behaviour*, 126, 53–67. <https://doi.org/10.1016/j.anbehav.2017.01.013>
- Stamps, J. A., & Luttbeg, B. (2022). Sensitive period diversity: Insights from evolutionary models. *The Quarterly Review of Biology*, 97(4), 243–295. <https://doi.org/10.1086/722637>
- Stephens, D. W. (1991). Change, regularity, and value in the evolution of animal learning. *Behavioral Ecology*, 2(1), 77–89. <https://doi.org/10.1093/beheco/2.1.77>
- Strambi, C., Cayre, M., & Strambi, A. (1999). Neural plasticity in the adult insect brain and its hormonal control. In K. W. Jeon (Ed.), *International review of cytology* (Vol. 190, pp. 137–174). Academic Press. [https://doi.org/10.1016/S0074-7696\(08\)62147-6](https://doi.org/10.1016/S0074-7696(08)62147-6)
- Tariel-Adam, J., Luquet, É., & Plénet, S. (2023). Sensitive windows for within- and trans-generational plasticity of anti-predator defences. *Peer Community Journal*, 3, e71. <https://doi.org/10.24072/pcjournal.304>
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20(4), 410–433. <https://doi.org/10.1111/j.1439-0310.1963.tb01161.x>
- Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14(1), 249–264.
- Walasek, N., Frankenhuis, W. E., & Panchanathan, K. (2022a). An evolutionary model of sensitive periods when the reliability of cues varies across ontogeny. *Behavioral Ecology*, 33(1), 101–114. <https://doi.org/10.1093/beheco/arab113>
- Walasek, N., Frankenhuis, W. E., & Panchanathan, K. (2022b). Sensitive periods, but not critical periods, evolve in a fluctuating environment: A model of incremental development. *Proceedings of the Royal Society B*, 289(1969), 20212623. <https://doi.org/10.1098/rspb.2021.2623>
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Additional technical details concerning the models that are part of our synthesis.

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