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

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Abstract

Sensitive periods, during which experiences have a large impact on phenotypic development, are most common early in ontogeny, yet they also occur during later ontogenetic stages, including adolescence. At present, however, we know little about why natural selection favors 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. Across formal 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 also emerge beyond early ontogeny when cues at later stages reduce this uncertainty more than earlier cues do. 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 highly reliable information from peers in adolescence to reduce uncertainty about the current and future social environment (e.g. social dominance, mate value). Finally, we highlight current gaps in our understanding, describe how different ways of quantifying sensitive periods influenced observed patterns, 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: sensitive periods, phenotypic plasticity, adolescence, modeling, evolution, development

Plasticity beyond early ontogeny

Plasticity – the ability of organisms to adjust their phenotypes based on experience (West-Eberhard, 2003) – is common early in ontogeny, yet also exists at later developmental stages, including adolescence. Adolescence corresponds to the period during which individuals experience physiological changes of puberty, paving the way towards sexual maturity (Reddy et al., 2022). More broadly, it can be defined as the transition towards independence from caregivers (Romeo et al., 2016). The retention of plasticity through adolescence and into adulthood has been documented across various taxa, including primates, rodents, birds (Fuchs & Flügge, 2014), reptiles, amphibians (Powers, 2016), fish (Ganz & Brand, 2016), and insects (Eriksson et al., 2019; Strambi et al., 1999). For example, humans, rodents, and birds show high levels of plasticity during adolescence in the development of social behaviors and social learning (Dahl et al., 2018; Fuhrmann et al., 2015; Laursen & Hartl, 2013; Ruploh et al., 2013; Sachser et al., 2018, 2020). Adult lizards are able to adjust their social behaviors (e.g. sharing refuges overnight) in semi-natural conditions even after having been reared in isolation for the first 1.5 years of their lives (Riley et al., 2018). Some frog species show plasticity in their locomotor system (i.e. body tissues and organs responsible for movement) in response to temperature changes as adults (Wilson et al., 2000). And, in some fish species, adult plasticity may underlie the restructuring of dominance hierarchies and induction of sex changes (Maruska & Fernald, 2013; Perry & Grober, 2003).

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 rapidly 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?

Understanding sources of variation in sensitive periods

Over the past several decades, there has been growing interest in the genetic, neurophysiological, and environmental sources of adaptive 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 made great strides in mapping the neurophysiological mechanisms underlying variation in sensitive periods. Recently, these advances have made it possible to experimentally reopen sensitive and critical periods (i.e. periods of heightened plasticity during which plasticity ceases) for specific experiences in certain species (Gabard-durnam & Mclaughlin, 2020; Hensch & Bilimoria, 2012; Nelson & Gabard-Durnam, 2020; Reh et al., 2020). And, biologists have studied how environmental conditions and experiences 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.

Nevertheless, 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., 2011, 2013; Zimmermann, Kaiser, Hennessy, et al., 2017; Zimmermann, Kaiser, & Sachser, 2017). 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. Can we identify environmental conditions that select for sensitive periods early or later in ontogeny? For instance, what rates of change in parameters of the social environment (e.g. sex ratio) or the physical environment (e.g. food abundance) might favor the evolution of sensitive periods in adolescence? In this paper, we discuss recent mathematical modeling addressing such questions, focusing on sensitive periods emerging beyond early ontogeny.

The paper is structured as follows. First, we introduce mathematical modeling of the evolution of sensitive periods. Then, we present explanations for sensitive periods beyond early ontogeny suggested by these models and establish links with empirical examples. Next, we describe how different ways of quantifying sensitive periods could influence observed patterns. Finally, we conclude by highlighting insights as well as existing gaps, and by presenting future directions addressing these gaps.

Modeling the evolution of sensitive periods

Although there is a longstanding and well-developed mathematical theory on the conditions that favor phenotypic plasticity (reviewed in Snell-Rood & Steck, 2019), only recently have theoreticians begun to explore why and how levels of plasticity change across ontogeny (Frankenhuis & Panchanathan, 2011; reviewed in Fawcett & Frankenhuis, 2015; Frankenhuis & Walasek, 2020). This work provides insights into the effects of experience on the features of sensitive periods, such as their timing and duration. These models thus advance our understanding of *why* variation in sensitive periods exists, complementing genetic, neurophysiological, and developmental insights about *how* it is instantiated.

Sensitive period models typically conceptualize development as a sequential decision-making process. Organisms are born with a prior estimate about their environment (e.g. safe or dangerous; resource-abundant or resource-poor). Throughout ontogeny organisms sample cues that provide imperfect information about the environmental state and develop phenotypes accordingly. The extent to which cues accurately reflect environmental conditions is often called the 'cue reliability' (or 'cue validity'). All models that we know of consider how sampled cues shape the information state of the organism. Some models additionally consider how changes in the information state (e.g. increased estimate about the presence of predators) translate to phenotypic adjustments (e.g. development of defenses) (e.g. Fischer et al., 2014; Frankenhuis & Panchanathan, 2011; Walasek et al., 2022a, 2022b). For different combinations of priors and cue reliabilities, these models then compute optimal phenotypic decisions that maximize survival and reproductive success (i.e. biological fitness) of the developmental system. In sequence, such decisions constitute optimal developmental trajectories. A robust finding across models is that plasticity tracks organism's uncertainty about the environment: the higher organism's uncertainty at birth and the more cues during ontogeny reduce this uncertainty, the higher plasticity tends to be early in ontogeny (Fawcett & Frankenhuis, 2015; Fraley & Roisman, 2015; Frankenhuis & Fraley, 2017; Frankenhuis & Walasek, 2020).

Bridging theory and data

Theoretical models can do more than expose the selection pressures shaping sensitive periods; they also provide testable empirical hypotheses. For example, drawing on Bayesian models of development (Stamps & Krishnan, 2014b, 2014a, 2017), one study has tested the 'discrepancy rule' (Stamps & Frankenhuis, 2016) in fruit flies (*Drosophila melangoster*). 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. Thus, individual differences in plasticity should be positively related to the discrepancy between priors and cues. Stamps et al. (2018)

found support for this prediction. They reanalyzed data from an aversive odor conditioning experiment in fruit flies (Saltz et al., 2017). In these experiments fruit fly larvae learn the association between an odorant (here acetate) and a negative stimulus (here an electric shock). Stamps et al. found that naïve individuals who were strongly attracted to the odor of acetate prior to conditioning reduced their attraction scores following aversive conditioning more than moderately attracted individuals.

Another study modeled and tested how different components of environmental change shape learning (Dunlap & Stephens, 2009). The model shows that an environment that changes predictably across generations selects for learning, while a stable environment with unreliable cues selects against learning. The authors then tested these predictions in fruit flies (*Drosophila melangoster*). During the experiment adult fruit flies are presented with two egg-laying media; one flavored with orange and one with pineapple. One of the media is paired with an aversive odorant (here quinine). After this experience phase fruit flies can choose either medium (without quinine) for oviposition. Then, the experimenter will choose eggs from one of the media to create the next generation of flies. This setup allows the experimenter to manipulate how reliably quinine-pairing predicts the best egg-laying medium and whether the best choice changes across generations. In line with predictions, fruit flies experimentally evolved the ability to learn the best site for oviposition in predictably changing environments but not in stable environments with unreliable cues. Both of the described experiments, however, were not designed to test predictions about sensitive periods, as they only manipulated cues at one time period during ontogeny. To our knowledge, no studies have experimentally evolved sensitive periods in development. As we discuss later, this will be an exciting direction for future research.

Theoretical models have also provided adaptive explanations for observed patterns of sensitive periods. For example, previous modeling work has illustrated the selection pressures producing sensitive periods in the development of immune system tolerance (Metcalf et al., 2022). Insufficient exposure to harmless microbes during sensitive periods results in late-age immune system dysfunction when hosts (human and non-human animals) fail to acquire tolerance. However, being exposed to pathogenic microbes during sensitive periods can lead to adverse health outcomes. The model explores how this trade-off between tolerance acquisition and pathogen infection shapes the optimal sensitive period duration in different microbial landscapes. The model shows that declining microbial diversity – as reported in human populations – requires a longer window for tolerance acquisition and can thus cause immune dysfunction in species that have shorter windows (such as humans). This example underscores how understanding the evolution of sensitive periods across development can inform medicine.

Relatedly, there has been increasing interest in understanding how evolved responses to early-life experiences shape individual differences in health and well-being (Kuijper et al., 2019). For example, some work suggests that the developing fetus and infant uses information provided through the mother's placenta and breast milk to predict the long-term nutritional environment (Kuzawa, 2005). The underlying idea is that this information obtained from the mother integrates over a lifetime of her experiences and is more reliable than early-life experiences obtained by the infant (Dall et al., 2015; McNamara et al., 2016). However, this implies that the infant might be insensitive to interventions manipulating nutritional conditions early in life (Kuzawa & Thayer, 2011). Thus, to develop effective interventions that improve developmental outcomes, we need to understand how organisms have evolved to integrate information from different sources and timescales. Modeling the evolution of this developmental plasticity can help us better understand why individuals differ in their susceptibility to early-life experiences and guide the development of preventative medicine (e.g. the timing of interventions).

Sensitive periods beyond early ontogeny: theoretical insights and empirical connections

As noted, although most models to date tend to find sensitive periods early in ontogeny, recent models point to conditions that favor sensitive periods later in ontogeny (Fischer et al., 2014; Stamps & Krishnan, 2017; Walasek et al., 2022a, 2022b). It is not clear yet whether later sensitive periods are produced by the same or different selection pressures. Here, we address this question by synthesizing findings from theoretical models reporting sensitive periods beyond early ontogeny. Our synthesis fills a current gap because there have been fewer connections between theoretical and empirical literatures on sensitive periods *beyond early ontogeny*—as there have been for sensitive periods *early in ontogeny* (the more common pattern in theoretical and empirical work). Our synthesis of theoretical and empirical literatures on sensitive periods beyond early ontogeny is also *timely*, because these literatures are both growing areas of research across the biological and social sciences (Blakemore & Mills, 2014; Frankenhuis & Walasek, 2020; Gee, 2022; Lewis, 2022; Reddy et al., 2022; Sachser et al., 2020; Sisk & Gee, 2022).

We include models in our synthesis 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. This criterion serves to exclude models in which organisms sample a cue in the first period and develop a phenotype in the second *without* being able to acquire new information in the second period. Such models are well-suited to studying the evolution of phenotypic plasticity (Botero et al., 2015; Gabriel, 2006; Moran, 1992; Stephens, 1991), but cannot capture *changes in plasticity* over the course of ontogeny – as this entails the impact of cues differing across time periods. Third, the model produces sensitive periods beyond early ontogeny; that is, heightened plasticity towards the middle or end of ontogeny, rather than the highest levels of plasticity occurring at the onset of ontogeny (the typical pattern). We have found four models that meet these three 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, rather than at its onset. If a model also favored 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 adjust to cues over multiple time periods and show their highest levels of plasticity later in ontogeny. In addition to these criteria, we focused our selection on empirical examples which match the theoretical explanations implied by the models.

Throughout our paper, we use the term ‘ontogeny’ to denote the time window during which experiences (i.e. cues) are relevant to the development of the trait. Thus, we are referring to the ontogeny of a specific trait and not necessarily to the ontogeny of the organism (i.e. period during which an organism develops). The onset of ‘trait ontogeny’ does not necessarily coincide with 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 (Stamps & Luttbeg, 2022). Thus, when we observe sensitive periods later in ontogeny, such periods do not necessarily map onto adolescence (‘mid-ontogeny’) or adulthood (‘late ontogeny’) in animals. Whether it does, depends on the empirical trait in question. Figure 1 illustrates the relationship between trait ontogeny and overall ontogeny.

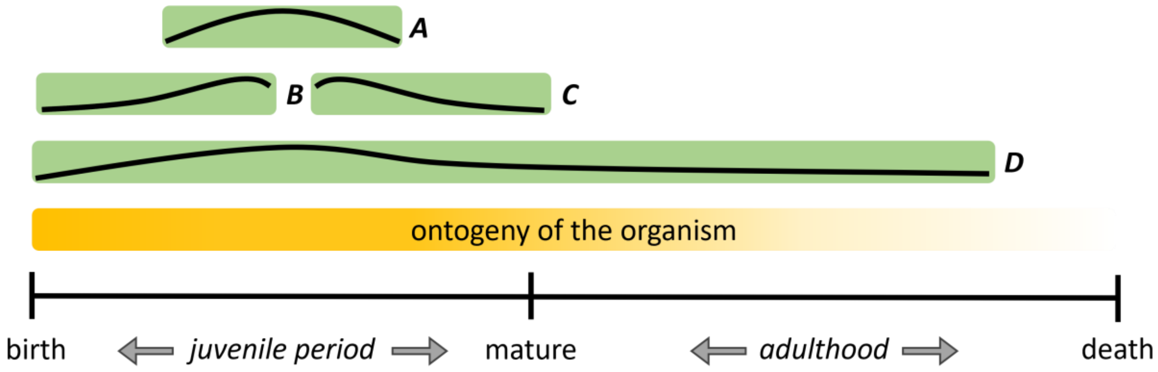

Figure 1. Trait ontogeny. This figure illustrates the relationship between trait ontogeny for different traits (light green boxes labelled A-D) and overall ontogeny of the organism (yellow box). The four traits (A-D) develop during different time periods. The black, curved lines indicate levels of plasticity across trait ontogeny. Relative to overall ontogeny the plasticity of all traits peaks around the same time. However, within their respective ontogenetic windows, traits A and D correspond to a mid-ontogeny sensitive period, B to a sensitive period at the end of ontogeny, and C to an early-ontogeny sensitive period.

Three explanations for sensitive periods beyond early ontogeny

Across the four models, we extracted three explanations for sensitive periods beyond early ontogeny: (1) increasing uncertainty about the environment over ontogeny, (2) increasing informativeness of cues across ontogeny, and (3) frequent changes in the environmental state throughout ontogeny. In what follows, we discuss these explanations and illustrate each one using empirical research across various species (Table 1). We also describe how the different study protocols for quantifying plasticity, used in theoretical and empirical research, influence the observed patterns of plasticity across ontogeny.

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, *Poecilia Formosa)*	Behavior 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) & reviewed in Hofmans & Van Den Bos (2022)
Various rodent species	Changes in aggression, exploration, and social play behavior in response to social defeat	Midway	Increasing cue reliability	Reviewed in Sachser et al., (2018)
Various rodent species	Social, anxiety-like, cognitive, and decision-making behaviors in response to social isolation	Midway	Increasing cue reliability	Reviewed in Li et al. (2021)
Bulb mites (*Rhizoglyphus robini*)	Male morph development in response to body size	End	Changing environment	Leigh & Smallegange (2014); Smallegange (2011)
Waterflea (*Daphnia magna*)	Size at maturity in response to short-term exposure to predator kairomones	End	Changing environment	Mikulski & Pijanowska (2010)
Paper wasps (*Polistes dominula*)	Nest-mate recognition in response to olfactory cues	End	Changing environment	Cappa et al. (2020)
Freshwater snail (*Physa acutas*)	Shell crush resistance in response to	End of ontogeny	Changing environments	Tariel-Adam et al. (2023)

	olfactory cues from predators			
Guinea pigs (*Cavia aperea f. porcellus*)	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 behavior and brain physiology in response to stress caused by changing, social environments	End or persisting plasticity	Changing environments	MacLeod et al. (2023)

Table 1: Empirical examples of sensitive periods beyond early ontogeny. Columns indicate the species, trait, pattern (midway vs. end of ontogeny), the theoretical explanation that best fits the example, and the reference. Note, that the theoretical explanation is at the ultimate level. That is, we hypothesize that a specific species may have experienced increases in uncertainty, changes in cue reliability, or changes in environmental conditions across ontogeny over evolutionary timescales. Therefore, natural selection has favored developmental mechanisms in those species that produce sensitive periods beyond early ontogeny. 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.

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

Three of the four models – Fischer et al. (2014), Stamps & Krishnan (2017), and Walasek et al. (2022) – produce sensitive periods mid-ontogeny because uncertainty increases early in ontogeny. However, the causes of this increase differ between these models. We will provide general qualitative insight in the main text and offer additional detail in Box 1.

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 prior. This results in sensitive periods early in ontogeny, but not at the onset (Figure 2, column 3, row 1 & 2, dark teal lines). When cues are low in reliability, organisms require more cues before adjusting phenotypes (row 1). Here, a smaller proportion of the population reaches sufficiently confident estimates of the environment to make costly adjustments, resulting in later and lower peaks in plasticity. Rapidly changing environments within generations (light teal line) amplify this effect further because phenotypic adjustments are potentially only useful for a short amount of time, resulting in low, 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 specialize towards the long-term environment indicated by the prior. Plasticity increases when some organisms sample cues that contradict their early estimates and increase uncertainty about the current fit with the expected future environment. On average, across all members of the population, such conditions result in mid- to late-ontogeny peaks in plasticity, driven by a subset of the population.

In Stamps and Krishnan (2017), the environment does not fluctuate across ontogeny. However, the authors explored scenarios in which organisms with priors indicating a highly dangerous environment, receive contradicting cues indicating a very safe environment. Similar to Fischer et al. and Walasek et al., 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 a peak in 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).

Empirical studies

Empirical evidence suggests that increases in uncertainty, particularly about the social environment, can result in sensitive periods mid-ontogeny (Table 1). 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. It is hypothesized that the perinatal period (i.e. pregnancy, lactation, and early parenthood) may similarly function as a window for stress-recalibration (Howland, 2023). This idea still remains to be tested. Increases in uncertainty may shape not only physiology, but also behavior. Recent experiments in humans have revealed an 'adolescent-emerging' increase in information sampling before making decisions (Ciranka & 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 generally 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., 2022). That said, it is currently unknown whether these observations generalize beyond the Western, industrialized populations typically studied.

Uncertainty might also shape plasticity in non-human animals. In one of humans' closest living relatives, the chimpanzee, adolescence – bringing about uncertainty and risk – is recognized as an important period for social exploration and learning (Reddy et al., 2022). However, such patterns also exist in non-primates. For example, a recent experiment in Amazon mollies (*Poecilia formosa*) revealed an initial increase in behavioral plasticity during the first weeks of life (Ehlman, Scherer, Bierbach, Stärk, et al., 2023). Amazon molly are a naturally clonal species and therefore an ideal model system for testing the development of individual differences. The fish were reared in benign, near-identical tanks to test the prediction that in stable environments plasticity peaks at the onset of ontogeny before monotonically decreasing. Thus, observing initial increases in plasticity conflicted with theoretical predictions. The authors suggest that a prey species, such as the Amazon molly, might enter the experiment with priors indicating a dangerous environment. As the fish start sampling cues indicating a safe environment, they become more uncertain about the state of the environment, causing increases in behavioral plasticity.

At a proximate level, 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; Jordan & Andersen, 2017; Scott & Frank, 2023). Such mismatches can occur when organisms explore novel or changing environmental conditions. While this literature has established the role of prediction errors in modulating neural plasticity, it is not clear whether prediction errors or sensitivity towards them vary across development. A study comparing human adolescents and adults found that adolescents showed faster learning from negative prediction errors compared to adults (Hauser et al., 2015), suggesting higher levels of plasticity in adolescence than adulthood. More studies considering the full breadth of development are needed to further clarify how the ability to learn from prediction errors changes across ontogeny, in humans as well as other species.

All but two of our empirical examples just discussed come from human studies. However, uncertainty has been recognized as a driver of personality-related differences in behavioral plasticity across various species and traits (Mathot et al., 2012). This work has not focused on how this inter-individual variation in levels of plasticity change across ontogeny. Thus, future studies covering multiple ontogenetic stages are needed to reveal uncertainty-related changes in plasticity, including inter-individual variation in these trajectories.

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: linearly increasing, first increasing and then decreasing ('triangular'), and linearly 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 predictive of the 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 organism's mate value (Fawcett & Frankenhuis, 2015). The higher the frequency of cues is, the more reliably organisms can use them to predict 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.

Empirical studies

Taken together, we should expect mid-ontogeny sensitive periods when reliable cues are more readily available during mid-ontogeny 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 seems to indicate sensitive periods for the development of social behavior 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 appear to 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 behaviors, 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 behaviors because of the availability of novel social landscapes. At a proximate level, neural restructuring during adolescence facilitates learning about these social landscapes.

In mammals, adolescence marks a novel developmental 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 cues that are suboptimal for their offspring. From an evolutionary perspective, 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 through their parents, the more scope there is for parents to shape their offspring's developmental trajectories in their own interest. Thus, adolescence offers an opportunity to sample cues that are more aligned with the developing offspring's own interests and may therefore more reliably predict their environment.

This influx of novel social experiences coincides with changes in brain structures relevant for social processing (reviewed in Hofmans & van den Bos, 2022). 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. Moreover, human adolescents are less likely to avoid ambiguity or punishment when learning about their environment, further promoting exploration (Raab & Hartley, 2019).

Combining insights across explanations for sensitive periods in adolescence, mammalian brains may have evolved to be ready for both increased uncertainty ('increasing uncertainty') and reliable cues ('increasing cue reliability') during adolescence. At a proximate level, the question is which factors initiate the onset of such sensitive periods. We have just presented empirical examples pointing to neurophysiological changes, as well as the availability of novel experiences and opportunities. Likely, both factors play a role in shaping plasticity but their contributions might vary for different traits. One principled way in which these factors might interact is through ‘metaplasticity’, the adaptive control of plasticity (Del Giudice, 2015; Frankenhuis & Gopnik, 2023; Scott & Frank, 2023; Soltani & Izquierdo, 2019; Tooley et al., 2021). In line with this theory, novel experiences and opportunities might modulate neurophysiological processes controlling levels of plasticity.

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 favor sensitive periods at the end of ontogeny (Figure 2, column 3, dotted light red lines). This finding is unique in comparison with all other models of the evolution of sensitive periods, not only the selection this paper focuses on. Notably, Fischer et al. (2014), who modeled environmental fluctuations in a similar manner as Walasek et al. (2022), 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 1). This assumption might more likely apply to morphological traits than to behavioral traits, which tend to be more malleable throughout life. However, not all morphological traits become fixed at a specific age (Burggren, 2020) and not all behaviors are plastic throughout the entire lifespan (Bell et al., 2009). Walasek et al.’s (2022b) assumption can also apply to cases where behavior remains plastic throughout the entire lifespan, when fitness effects are largest at a specific stage, such as the transition to adulthood (i.e. fitness is mainly accrued at the end of ontogeny). More generally, for traits that become fixed or accrue the largest fitness effects after maturation, developing organisms need to build phenotypes that match the long-term future environment. In these cases, it makes sense that organisms should be most sensitive to cues towards the end of ontogeny: when the environment changes frequently, cues towards the end of ontogeny are better predictors of the future environment (Tariel-Adam et al., 2023).

Empirical studies

There seem to be fewer examples in the empirical record 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 is representative of nature versus reflecting the focus of empirical researchers (e.g. on a subset of species). A third possibility is that researchers documenting sensitive periods late in ontogeny tend not to use the term ‘sensitive period' to describe their findings. For instance, a researcher of insects might study a species that only responds to a particular environmental cue in later stages of metamorphoses, without describing such a response as a 'sensitive period'. In fact, although most of the examples we have discussed so far involve humans and rodents, there are clear examples of sensitive periods late in ontogeny in a range of other animals, including mites, water fleas, wasps, and snails (Table 1). Also, the sensitive periods in these animals cover a broader array of traits than we have covered so far, such as offensive and defensive morphologies.

An interesting possibility is that sensitive periods in late ontogeny tend to occur in species that undergo major transformations across life stages (e.g. metamorphosis). Consider morph development in male bulb mites (*Rhizoglyphus robini*). Experimental research shows that whether males mature as fighters or benign, defenseless 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. Bulb mites who temporarily experience lower-quality food during the protonymph stage, cannot compensate for lost growth if given richer foods during the final instar stage (Leigh & Smallegange, 2014). Thus, we may hypothesize that size at the end of ontogeny summarizes environmental conditions across ontogeny and helps predict future environmental conditions, favoring a late sensitive period for male morph development.

Another clear 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. 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 maturation 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 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 offspring before being eaten. Relatedly, a recent experiment in freshwater snails (*Physa acuta*) revealed a late-ontogeny sensitive period for developing shell crush resistance (Tariel-Adam et al., 2023). Snails who were exposed to predators during late ontogeny developed higher shell crush resistance compared to controls who never encountered predators. During this late ontogenetic window snails are likely to reach sexual maturity. Thus, stronger predator defenses might be particularly important during this time. However, although the crush resistance was descriptively highest for late-exposed individuals, it did not significantly differ from other exposure windows (embryo, early ontogeny, mid-ontogeny) aside from controls. Future replications are needed to determine the exact timing and duration for this sensitive period.

Sensitive periods in early adulthood also occur for social behaviors. Recent work in paper wasps (*Polistes dominula*) shows that nest-mate recognition is shaped primarily by the adult social context, rather than, as previously thought, by genetic cues or early experiences. In rodents, the evidence for sensitive periods in social behaviors 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 (environmental enrichment) (Freund et al., 2013, 2015; Heller et al., 2020; Kempermann et al., 2002; Lefeuvre et al., 2023; Sherry & Hoshooley, 2010).

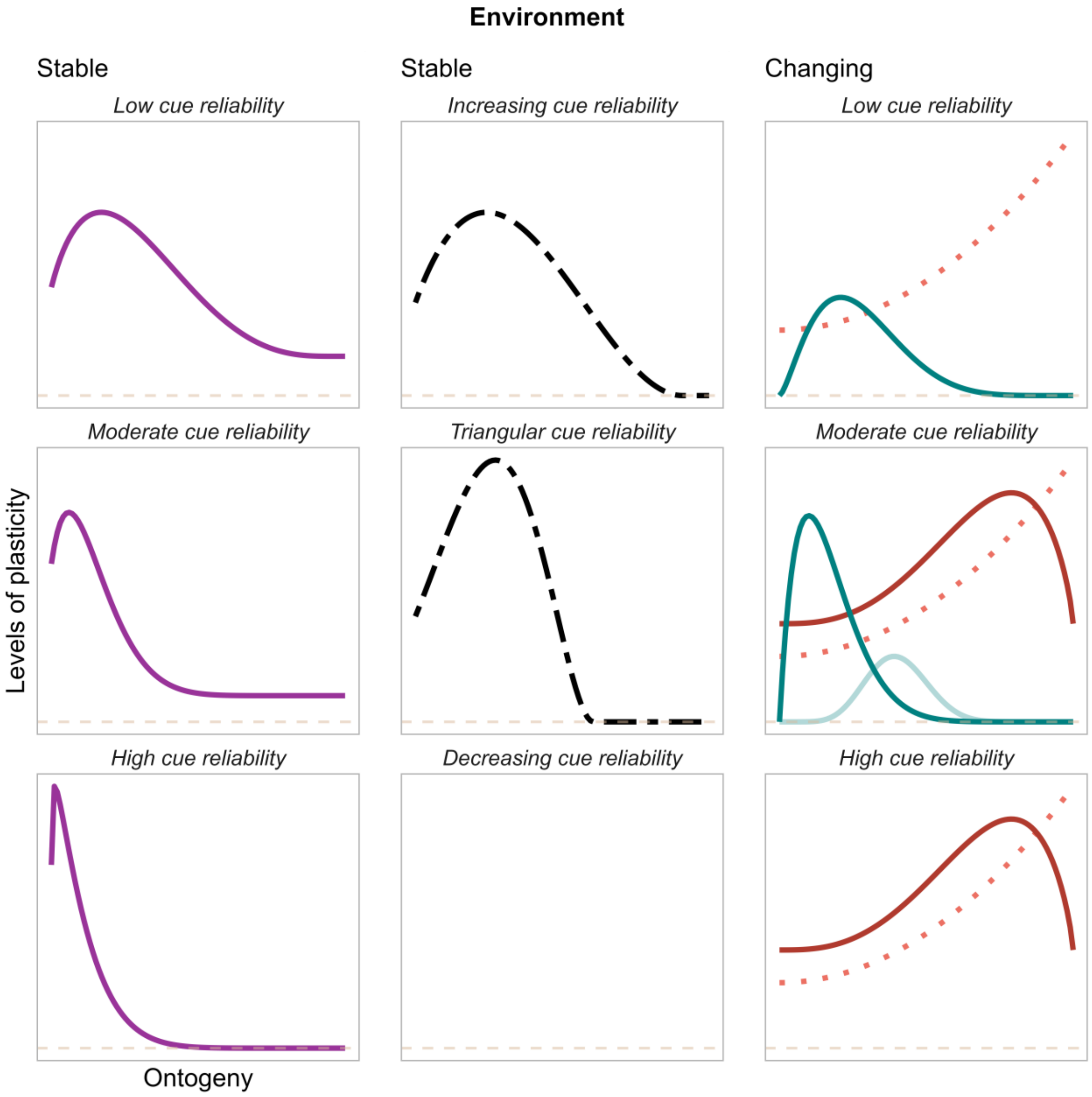

Figure 2: Explanations for sensitive periods beyond early ontogeny across models. Rows and columns indicate environmental conditions in the models. Rows depict the level (low, moderate, high) or pattern of cue reliability (increasing, triangular, decreasing). Columns depict whether the environmental state is stable or might change within an individual's lifespan. Colors indicate the four models we focus on: in purple, Stamps & Krishnan (2017); in black, Walasek et al. (2021); in red, Walasek et al. (2022); and in teal, Fischer et al. (2014). Line types indicate different explanations; solid: increases in uncertainty, double-dash: increases in cue reliability, and dotted: changing environments. Color intensity indicates the rate of environmental change (only relevant for third column); light: fast and dark: slow. 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. Thus, individuals within a population may deviate from this average pattern.

The timing of trait ontogeny relative to overall ontogeny

We hypothesize that the theoretical explanations for sensitive periods beyond early (trait) ontogeny should, almost always, hold irrespective of when the trait develops (Figure 1). However, the specific timing of trait ontogeny may exclude some possible explanations for why the reliability of cues could change across ontogeny (Explanation 2). For example, changes in the reliability of cues cannot be explained by sensory development if the trait only develops after sensory maturation.

The third explanation, proposing sensitive periods towards the end of ontogeny due to frequently changing environments, might not be valid for all trait ontogeny windows. Whether it is, depends on the gap between a trait's development and its impact on fitness. Suppose a trait develops right after birth but fitness consequences only accrue after maturation. Under such conditions, cues towards the end of the ontogeny of the trait might not be good predictors of environmental conditions after maturation. However, the closer the end of trait ontogeny is to the window during which fitness accrues, the more likely cues at the end of trait ontogeny predict the relevant future environment.

Shared principled in reasons for sensitive periods beyond early ontogeny

Looking across models, we observe two, broad explanations for sensitive periods beyond early ontogeny. These periods emerge (a) when an organism's uncertainty about the environment-phenotype fit increases later in ontogeny, and (b) when cues later in ontogeny reduce this uncertainty more than earlier cues do. Figure 3 illustrates these two explanations from the point of view of a focal individual (guinea pig with black patches). As is typical in mammals, juvenile guinea pigs depend on parental care and receive cues about their environment from their parents (e.g. about the density of predators). Once guinea pigs become independent from their parents, they are able to sample cues from peers about their position in the social hierarchy and their value as a mate. Plasticity peaks in adolescence (a) when individuals start to receive more reliable cues to their mate value in the form of social feedback from peers. Plasticity peaks or persists in adulthood (b) when adult guinea pigs experience uncertainty about their fit with the social environment due to changes in the composition of males (blue patches) to females (pink patches).

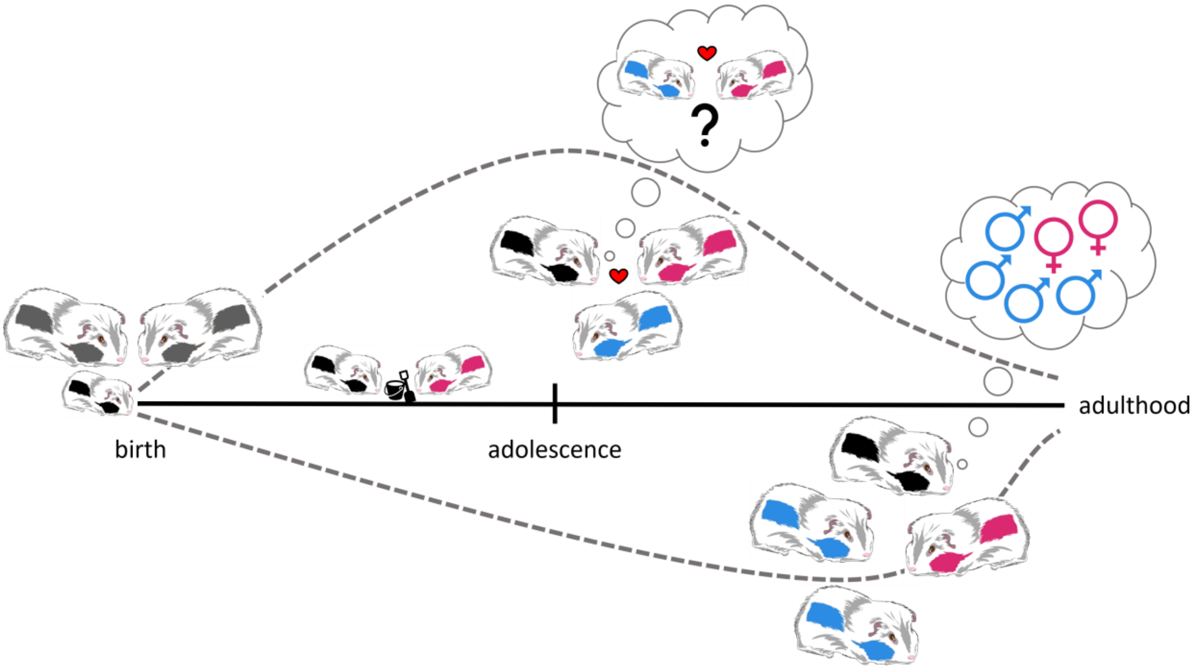

Figure 3. Plasticity tracks uncertainty across ontogeny. The x-axis depicts ontogeny for social behaviors in guinea pigs. Grey dashed lines depict hypothetical trajectories of plasticity. Sensitive periods later in ontogeny emerge when (a) later ontogenetic stages coincide with organisms being particularly uncertain about the current state of their environment. Or, when (b) cues at later in ontogeny are particularly reliable, enabling the organisms to reduce their uncertainty about the state of their environment. This figure illustrates both situations. Guinea pig icons are based on the following, copyrighted artwork and have been adjusted by the authors. Copyright: guineapig-white icon by Servier https://smart.servier.com/ is licensed under CC-BY 3.0 Unported https://creativecommons.org/licenses/by/3.0/.

Are sensitive periods in mid-ontogeny an artifact of the study protocol?

Whether a specific model produces sensitive periods beyond early ontogeny might, in part, depend on the study protocol used to measure plasticity (Stamps & Luttbeg, 2022; Walasek et al., 2022a). That is, the same model could lead to different conclusions about the timing of plasticity depending on the study protocol. Understanding the role of the study protocol is thus important for interpreting and comparing results from different models, and for linking findings to empirical studies.

Walasek et al. (2022a) and Stamps & Luttbeg (2022) examined three different protocols for measuring plasticity. These protocols share a basic paradigm that resembles empirical approaches. Suppose a researcher wants to measure how housing conditions throughout ontogeny shape aggression in guinea pigs. They might manipulate animals' housing conditions at different developmental stages: for example, in juveniles, early adolescents, late adolescents, and adults. For comparison, they would also maintain a control group, which has experienced standard housing conditions throughout ontogeny. Before running the experiment, the researcher will need to consider two questions. First, how long should guinea pigs remain in treatment housing conditions: for a temporary amount of time or until the end of ontogeny (treatment duration)? Second, when should they measure differences in aggression between treatment and control individuals: right after the treatment or at the end of ontogeny (measurement time)? Models of sensitive periods typically use protocols that cover different combinations of treatment duration and measurement time. We detail how each of the four models in our synthesis measured plasticity in Box 2.

Both Stamps & Luttbeg (2022) and Walasek et al. (2022a) observe that a protocol in which phenotypic differences are assessed after a temporary treatment condition may be more likely to produce mid-ontogeny sensitive periods compared to other protocols. Stamps & Luttbeg also reanalyzed empirical data from an experiment in tadpoles (Relyea, 2003) and confirm that different protocols lead to different conclusions. Thus, we need to be mindful of the protocol(s) used when interpreting empirical data. That protocols matter also means we should be careful when stating model predictions. In some cases, a model might predict a mid-ontogeny sensitive period only if plasticity is measured a certain way.

In their paper, Stamps & Luttbeg (2022) highlight how empirical studies do not consistently use the same protocol, making it difficult to derive conclusions about patterns of plasticity across different traits or species. We also observe such inconsistencies across the models that are part of our synthesis. On the one hand, it would be easier to aggregate if all empirical and theoretical studies used the same protocol. On the other hand, different protocols might provide different insights. Generally, a researcher should choose a protocol that best captures a specific research question. Specifically, the adoption protocol can capture *long-term* effects of *continued* exposure to experiences. In contrast, the plasticity and window protocol are suitable for capturing the *short-term* (for the plasticity protocol) and *long-term* (for the window protocol) effects of *temporary* exposure to experiences. In principle, short- and long-term effects of temporary exposure can be studied within one experiment by incorporating multiple treatment durations and measurement times. Such work would be a valuable direction for future research.

Sensitive periods beyond early ontogeny: Insights and gaps

Our synthesis offers three main insights. First, models suggest that natural selection may favor levels of plasticity to track organisms' uncertainty and the potential of cues to reduce it. We may expect sensitive periods beyond early ontogeny if organisms are more uncertain at later developmental stages and when cues later in ontogeny can help to reduce this uncertainty. Second, our selection of models and empirical examples includes more cases of sensitive periods mid-ontogeny than towards the end of ontogeny. Third, most empirical examples of sensitive periods beyond early ontogeny involve social behavior in mammals. At present, we do not know whether sensitive periods in mid-ontogeny are more common in mammals, or whether researchers have understudied other life stages, species, and traits. Future systematic reviews and meta-analyses can distinguish between these possibilities.

We have also identified three gaps in our current understanding of sensitive periods beyond early ontogeny. First, it is challenging to aggregate and compare findings across theoretical and empirical studies because they vary in their conceptual and methodological approaches to studying plasticity. Second, we lack empirical studies specifically designed to test predictions from sensitive period models. Third, only a handful of models have explored sensitive periods later in ontogeny and these models do not incorporate recent empirical insights (e.g. about adolescence being a sensitive period for social behaviors). In the final section, we suggest future directions to address these gaps and strengthen connections between theoretical and empirical studies.

Future directions and conclusion

The study of sensitive periods would benefit from harmonization of methods. This is true both for empirical and theoretical studies. For the longest time the predominant view was that sensitive periods occur mainly early in ontogeny. Recently, researchers have started to explore sensitive periods beyond early ontogeny, adopting different approaches. We think that such initial variation in approaches may be a good thing. With time and experience, we can learn about the insights that different approaches can offer. However, as the field matures, it would benefit from increased standardization. As noted earlier, integration of findings across models would benefit from a shared framework for measuring plasticity (section ‘Are sensitive periods in mid-ontogeny an artifact of the study protocol?’). It would also be helpful if empirical studies could provide more details about the natural ecology of the animal and types of cues they use. For example, empirical studies of sensitive periods do not routinely report whether and at what rate the environment – to which the focal trait might be adjusting – changes across ontogeny. Knowing such ‘environmental statistics’ will make it easier to link empirical and theoretical studies (Burgess & Marshall, 2014; Frankenhuis et al., 2019; Hartley, 2022; Marshall & Burgess, 2015).

We can deepen our understanding of sensitive periods by designing new empirical studies. Although many empirical studies explore 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 for different species and traits, we need experiments covering multiple ontogenetic stages. To establish a sensitive period at the onset of ontogeny, a minimum of two measurement times is needed. However, to establish a sensitive period mid-ontogeny we need at least three measurement times to make the necessary comparisons (onset vs mid and mid vs late). In an ideal world, 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, are bringing us closer to this ideal scenario (Dupont et al., 2023; Ehlman, Scherer, Bierbach, Francisco, et al., 2023; Kievit et al., 2021). Earlier, we presented a study in Amazon mollies (*Poecilia Formosa*) which demonstrates the potential of these advancements: using high-resolution tracking tanks, the authors near-continuously quantify plasticity in behavioral phenotypes across ontogeny (Ehlman, Scherer, Bierbach, Stärk, et al., 2023).

High-resolution and multidimensional data of the environment and phenotypes presents an excellent resource for studying interactions between animal personality and phenotypic plasticity (Bell et al., 2009; Dingemanse et al., 2010; Mathot et al., 2012). Such data affords quantifying how different behaviors covary across development. Extending experiments to cover multiple generations can additionally provide answers to questions about sensitive periods for transgenerational plasticity (Tariel-Adam et al., 2023; Uller et al., 2013). That is, during which ontogenetic windows do parents' experiences induce phenotypic changes in the next generation? However, we must also acknowledge that implementing a workflow that can track animals continuously and process such large amounts of data is challenging.

Another important empirical future direction is to experimentally test model predictions about sensitive periods later in ontogeny. Experimental evolution offers unique opportunities for testing predictions from theoretical models. This approach typically uses species with a short generation time to study how controlled manipulation of the environment (e.g. cues) shape evolution. Earlier, we described two studies that have successfully tested theoretical predictions through experimental evolution (Dunlap & Stephens, 2009; Stamps et al., 2018). We currently lack similar studies that manipulate experiences across multiple time periods. Insect and invertebrate model systems are particularly well-suited to reducing the gap between theoretical predictions and empirical insights about sensitive periods (e.g. English & Barreaux, 2020).

To increase synergies between empirical and theoretical studies, future models could incorporate existing empirical insights. The models reviewed here are agnostic about the type of experience organisms face (e.g. positive vs. negative) and the specific trait they develop (e.g. a defense against predators or a specific social trait). Future work can extend existing evolutionary models by explicitly implementing novel empirical insights about specific traits or classes of traits (e.g. social behaviors) (Frankenhuis et al., 2018; Kacelnik, 2012; McNamara & Houston, 2009; Trimmer et al., 2012). For example, we could incorporate recent insights about sensitive periods for social traits into prior modeling work on the evolution of helping behaviors (Kuijper & Johnstone, 2019). This model explored the development of helping behaviors only in response to early-life stress. An extension of this work could explore plasticity in response to social experiences (both negative and positive) later in ontogeny as well.

There is a dearth of models exploring the evolution of sensitive periods beyond early ontogeny in the context of social dynamics. The models in our synthesis provide insights about how the physical environment influences sensitive periods later in ontogeny. We have used these insights to explore adaptive explanations for behavior in general, including social behavior. For example, we speculated that frequent changes in the social environment (e.g. changes in the sex ratio) may favor heightened plasticity in adolescent guinea pigs. However, the field actually needs models that explicitly incorporate social dynamics among individuals to rigorously explore the plausibility of this explanation. Thus, there is great scope for future modeling to explore how characteristics of the social environment shape sensitive periods beyond early ontogeny. This work could, for example, provide novel insights into how social context shapes foraging strategies and nest-building in birds (Breen et al., 2020; Franks et al., 2020)

Existing models can also be extended by incorporating variation in fitness benefits across ontogeny. In many species survival and fertility are likely more strongly shaped during some life stages than others. For example, it is conceivable that adjusting morphological features shortly before the onset of adulthood could increase survival and reproduction (e.g. as seen in Mikulski & Pijanowska, 2010). Similarly, tailoring social behaviors to the adolescent social environment likely influences future reproductive success (Sachser et al., 2020). A formal investigation of these ideas is lacking. Future models of sensitive periods could capture these phenomena by letting fitness benefits vary across ontogeny (Houston et al., 1988; Mangel & Clark, 2019). Modelers may then explore how increased or lowered fitness benefits at specific life stages shape patterns of sensitive periods.

Lastly, models of sensitive periods to date have barely explored life-history trade-offs. Yet, several of the empirical patterns in Table 1 may reflect trade-offs between fertility and survival. Consider, for instance, water fleas (*Daphnia magna*) maturing smaller to lower the chance of being eaten by a predator before reproducing (Mikulski & Pijanowska, 2010). Life-history trade-offs might also be involved in shaping the different male morphs (fighters vs. scramblers) in bulb mites (*Rhizoglyphus robini*) (Deere & Smallegange, 2023; Smallegange et al., 2019). For example, in poor environmental conditions benign scramblers may be at an advantage because they can reach sexual maturity faster than fighters. How these trade-offs shape male morph development is not yet understood. Future models of sensitive periods could provide insights by incorporating life-history trade-offs, for example, by allowing individuals to choose when to terminate ontogeny for a specific trait and/or transition into the next life stage.

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.

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Box 1 – Models of sensitive periods

Although all four models in our synthesis report sensitive periods at later life stages, they vary in their assumptions. We can coarsely categorize the models along four dimensions: (1) whether phenotypes are explicitly modeled (‘belief-only’ vs ‘belief-and-phenotype’), (2) when fitness accrues (throughout vs at the end of ontogeny), (3) whether the environment is stable or fluctuating across ontogeny, and (4) whether phenotypic traits develop incrementally or unrestricted.

All four models consider how information obtained from cues shapes the information state (‘belief’) of the organism. Fischer et al. (2014) and Walasek et al. (2022a, 2022b) additionally consider how changes in the information state (e.g. increased estimate about the presence of predators) translate to phenotypic adjustments (e.g. development of defenses). In contrast, Stamps and Krishnan (2017) assume a one-to-one mapping between organisms’ estimates of the environment and their phenotypes. We thus refer to Stamps and Krishnan (2017) as a ‘belief-only’ model and to the other three models as ‘belief-and-phenotype’ models. For different evolutionary ecologies, belief-and-phenotype models compute optimal phenotypic decisions that maximize survival and reproductive success (i.e. biological fitness) of the developmental system. In Fischer et al. (2014) organisms accrue fitness throughout ontogeny while in Walasek et al. (2022a, 2022b) organisms accrue fitness only at the end of ontogeny.

The four models also differ in their assumptions about the environment and how organisms develop. Stamps and Krishnan (2017) and Walasek et al. (2022a) assume that the environment remains stable across ontogeny. The other two models (Fischer et al., 2014; Walasek et al., 2022b) assume that the environment fluctuates between two possible states across ontogeny. The two models by Walasek et al. (2022a, 2022b) assume that phenotypic development is incremental, meaning that individuals gradually adjust their phenotypes across ontogeny. By contrast, Stamps and Krishnan (2017) and Fischer et al. (2014) assume unrestricted phenotypic development, such that organisms can freely adjust phenotypes in any direction and to any extent within just one time period. In the main text we discuss how these differing assumptions shape qualitative patterns in models of sensitive periods.

Box 2 – Quantifying plasticity

The current body of models exploring sensitive periods uses a variety of study protocols to quantify plasticity. Stamps & Krishnan (2017) and Fischer et al. (2014) quantify plasticity as the phenotypic difference between two consecutive time periods in response to a single cue. While Fischer et al. do not explore different manipulations of cues, Stamps & Krishnan study different kinds of cues as ‘treatment’ conditions. For example, an organism may be first exposed to cues indicating a safe environment before receiving a cue indicating a dangerous environment (i.e. the treatment cue). Plasticity then corresponds to the posterior difference before and after exposure to this cue. Walasek et al. (2021, 2022) use an adoption protocol in which organisms get separated at some point during ontogeny. Before separation organisms develop together and are clones of one another. At some point during ontogeny one of the clones is taken away to a ‘treatment patch’ in which it receives opposite cues compared to its original counterpart until the end of ontogeny. Plasticity then corresponds to the phenotypic difference between separated clones at the end of ontogeny. The larger this difference, the more clones were shaped by cues during their separation, suggesting a high degree of plasticity at the onset of separation—when cues began to diverge.

Additionally, Walasek et al. (2021) consider two different types of plasticity: *absolute* and *relative* plasticity. The former corresponds to the absolute magnitude in phenotypic differences. We define the phenotypic distance between two individuals as the Euclidean distance along these two dimensions (i.e. the square root of the sum of the squared differences). The latter normalizes this differences by considering the amount of time that clones developed together. Walasek et al. (2021) consider the latter to capture the potential for plasticity after controlling for phenotypic similarities due to initial shared experiences and the shorter time horizon for developing phenotypic differences. Overall, these different ways for quantifying plasticity may be captured along the following dimensions: treatment cues, duration of treatment, and time of measurement as described in Figure 1.

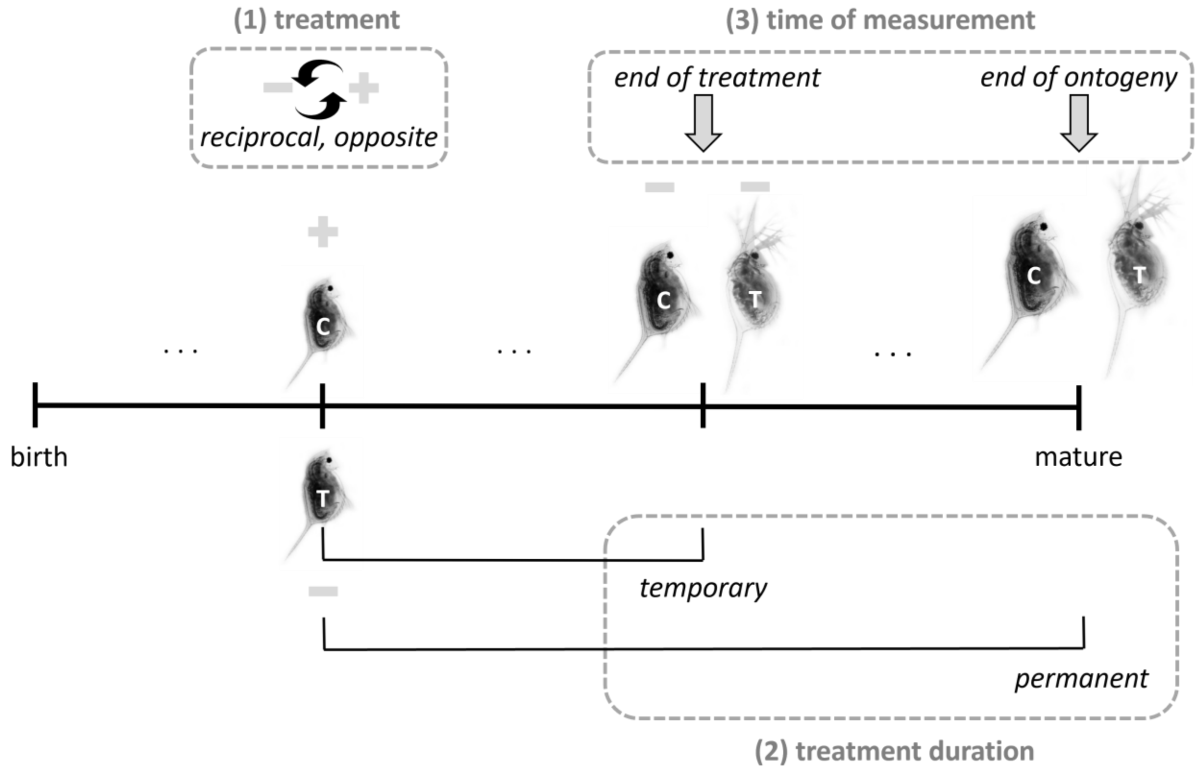

Figure 1. **Quantifying plasticity**. Plasticity is typically quantified as within-genotype differences in phenotypes in response to cues. Different types of protocols for inducing such phenotypic differences can be captured along three dimensions. First, the treatment describes the kinds of cues to which individuals are exposed to. For example, phenotypic differences may be assessed between a control ('C') and a treatment individual ('T') who has been exposed to reciprocal, opposite cues compared to the control individual. Second, the duration of such a treatment may vary. It may be permanent, lasting until the end of ontogeny, or only temporary. After a temporary treatment, the control and treatment individual will receive the same cues again. Third, we can specify when phenotypic differences are measured. We may either measure them at the end of the treatment or at the end of ontogeny.
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