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Who cares? An integrative approach to understanding the evolution of behavioural plasticity in parental care

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Natural selection acts on underlying mechanisms to fine-tune expression of behaviour across scales – within individuals, among individuals, between sexes and across species. The inherently environmentally responsive nature of behaviour, or behavioural plasticity, may bias how behaviour evolves. However, studies of plasticity rarely integrate patterns across levels of biological organization and timescales, limiting our understanding of how mechanisms of individual behavioural variation translate to patterns of evolutionary diversification. Here, we advocate that the contributions of plasticity to evolution between populations and species cannot be fully understood without consideration of plasticity within and between individuals; particularly in view of the often assumed but rarely tested idea that mechanisms mediating plasticity are the same as those targeted by selection. Using parental care as a touchstone, we explore how mechanisms involved in behavioural plasticity in individuals may (or may not) be co-opted to generate behavioural variation among individuals, between sexes and across species. We draw on parental care diversity in poison frogs to explore how different patterns across levels of biological organization inform our predictions of evolutionary outcomes and advocate for more empirical studies of proximate mechanisms underlying individual variation. Alongside a renewed appetite for empirical studies of phenotypic plasticity, recent years have seen major technological advances that have made mechanistic studies increasingly possible, even in nonmodel systems. Parental care is only one example, and we emphasize that these concepts apply to the general conversation about the evolution of behaviour, behavioural plasticity and phenotypic plasticity more generally.

Although evolution ultimately relies on genetic change, environmentally induced phenotypic plasticity may bias evolutionary trajectories towards certain outcomes (West-Eberhard, 2003). The role of environmentally induced phenotypic change (i.e. phenotypic plasticity) in adaptation has been contentious since the inception of evolutionary biology, with debate as to whether and how phenotypic plasticity may facilitate adaptation and how plasticity itself evolves (for review see Foster, 1995, 2013; Ghalambor et al., 2007; Levis & Pfennig, 2016; Moczek et al., 2011; Price et al., 2003; West-Eberhard, 2003). While theoretical debate is long-standing, the field has recently seen a resurgence of interest in these questions, accompanied by a proliferation of empirical studies. New data suggest that plasticity can indeed facilitate adaptation (Ghalambor et al., 2015; Jeffery, 2008; Ledon-Rettig et al., 2013; Potticary et al., 2020), yet open questions remain.

A key idea championed by Susan Foster is that patterns in the evolution of plasticity may depend on the type of trait (Foster et al., 2015). In the case of morphological traits, flexible developmental starting points may facilitate modification of form and function in different environments. By contrast, behavioural traits are products of neural networks and endocrine systems, such that differences in behaviour tend to arise not from modulation of the pattern of response but rather the *degree* of responsiveness (Foster et al., 2015). These ideas helped advance the current consensus that we need to study underlying mechanisms to truly understand plasticity and its role in evolution (Alonzo, 2015; Duckworth, 2009; Duckworth & Sockman, 2012; Fischer et al., 2016; Snell-Rood, 2013; West-Eberhard, 2003).

Renewed interest in phenotypic plasticity has come alongside the genomic revolution of the past 20 years, which has provided new opportunities to study mechanisms in nontraditional model species particularly well suited to testing ideas about the role of phenotypic plasticity in evolution (Fischer et al., 2021). A critical open question is whether the mechanisms that facilitate plasticity at the individual level are the same as those ultimately targeted by

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selection to drive adaptation (Fig. 1; e.g. Levis & Pfennig, 2016). In other words, can mechanistic co-option explain how initially environmentally induced responses become genetically modified (i.e. genetic accommodation; West-Eberhard, 2003) or fixed (i.e. genetic assimilation; Waddington, 1959)? Despite the fundamental nature of this question, the integrative perspectives needed to satisfactorily answer it – considering both individual level plasticity and population level processes – are often lost in the 'search for a mechanism' (Duckworth, 2009; Forsman, 2015). Historical divides between scholars of behavioural ecology and evolutionary genetics verses neurobiology provide a likely explanation as to why calls for integration tend to fall short (Autry & O'Connell, 2021).

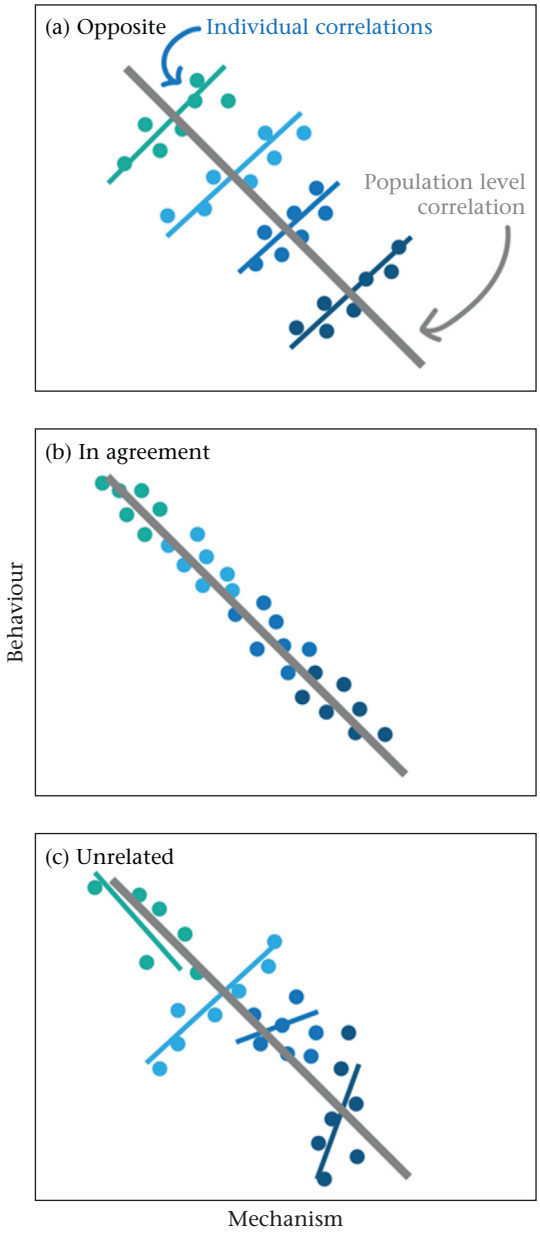

Figure 1. Relationships between behaviour and underlying mechanisms may differ across levels of biological organization. Correlations may follow (a) opposite patterns or (b) similar patterns, or (c) be unrelated. While often presented as a framework for relating within and among individual levels (e.g. Malkoc et al., 2022; Niemelä & Dingemanse, 2018), these concepts can apply across other scales as well (e.g. relating plasticity within and among behavioural states, sexes, or species). However, the pattern at one level/scale does not necessarily predict the pattern at a different level/scale (Adkins-Regan, 2005; Hau & Goymann, 2015; Malkoc et al., 2022; Niemelä & Dingemanse, 2018) and additional empirical work is necessary to understand whether a particular pattern prevails.

Even where studies succeed in bridging these disparate scales of investigation, it is difficult to derive generalities across taxa from limited empirical studies (Adkins-Regan, 2005; Niemelä & Dingemanse, 2018). For example, work in estrildid finches identified parallel nonapeptide patterns associated with sociality within and across species (Fig. 1b; Goodson et al., 2009; Goodson & Kingsbury, 2011); however, such parallelism has yet to be shown in other major radiations (Fig. 1c; e.g. cichlids; O'Connor et al., 2015) and in some cases the directionality of the association even reverses, moving from the intraspecific to the interspecific scale (Fig. 1a; Nowicki et al., 2020). Hence, some key questions remain. Is the genetic co-option of plastic mechanisms a common route to behavioural diversification? Are some mechanisms and molecules more likely to be targeted than others? Addressing these will require an approach championed by Susan Foster and recent calls for the development of model clades (Jourjine & Hoekstra, 2021): contrasting patterns of plasticity across recently diverged lineages in natural radiations.

One type of behavioural variation that has received considerable attention within species but has yet to be embraced as a major driver of diversification between species is variation between the sexes. West-Eberhard (2003) originally coined the term 'cross-sexual transfer' to describe the process whereby a trait initially expressed only in one sex is plastically induced, and subsequently genetically fixed, in the opposite sex – a process she ranked alongside duplication as an underappreciated force in the evolutionary origins of novelty. Male and female behavioural traits rely on remarkably similar neural, molecular and genetic machinery (Becker et al., 2007; de Vries & Södersten, 2009; Gegenhuber & Tollkuhn, 2020) and therefore provide a particularly exciting opportunity to understand how shared underlying mechanisms are differentially tuned to give rise to differences in 'sex-typical' behaviour, in the degree of behavioural plasticity within and between sexes and in the evolution of behavioural plasticity itself.

Here, we outline a multilevel perspective of the complex, variable relationships between plasticity and evolution. We argue that the contributions of plasticity to behavioural evolution between populations and species cannot be fully understood without consideration of plasticity within and between individuals, particularly in view of the long-held and increasingly testable idea that natural selection can co-opt mechanisms involved in environmentally induced changes (Hoke et al., 2019; Levis & Pfennig, 2016). We first describe how variation within and among individuals can emerge through mechanisms regulating the context and degree of expression of behaviour, and how this variation presents targets for selection. We then discuss how mechanisms underlying among-individual variation may contribute to the evolution of novel behaviour between sexes, populations and species. We focus on parental behaviour as a case study of cross-sexual transfer and an example of how integrating mechanisms into studies of behavioural plasticity can help bridge scales of empirical investigation, from individuals to species (Fig. 2). Throughout, we use the term mechanism to encompass any internal process (e.g. hormones, neural activation, regulation of gene expression) that transduces an external environmental cue into a behavioural response (phenotype), either by modulating the sensitivity with which the animal perceives the cue or how the cue is processed and translated. While an extensive review of the literature on behavioural plasticity and of specific mechanisms is beyond our scope, we provide examples of potential underlying mechanisms throughout and hope these examples will inspire further reading and mechanistic thinking in our readers. We advocate that exploration of underlying mechanisms is necessary for a more complete understanding of how

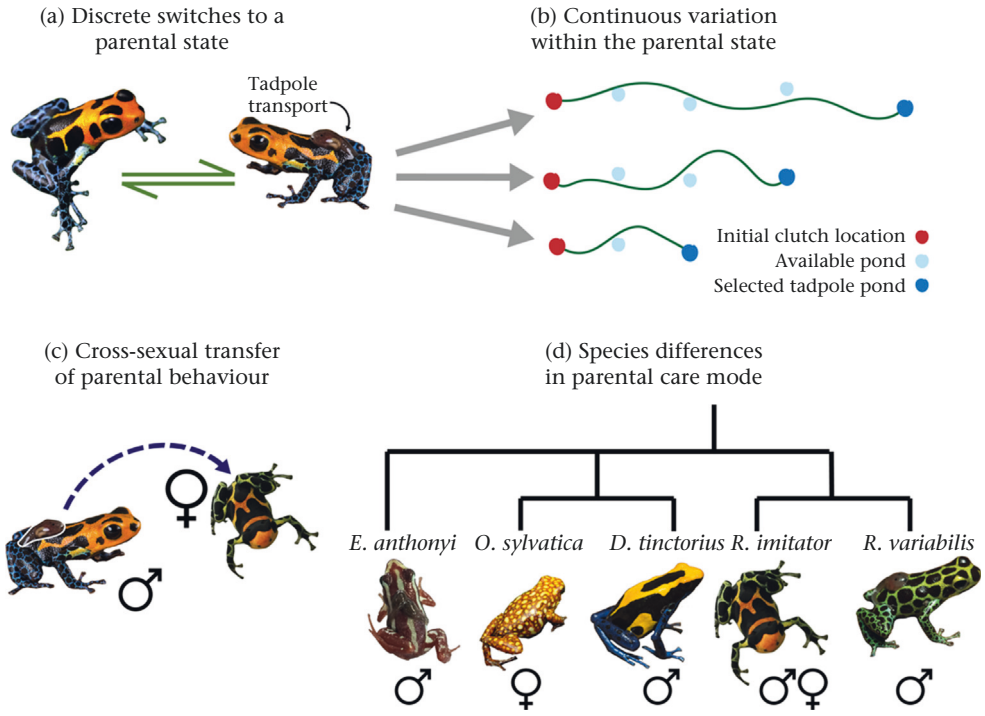

Figure 2. Behavioural plasticity can be studied across scales. For example, in poison frog parental care, we see (a) discrete switches to a parental state (e.g. when parents initiate tadpole transport) and (b) continuous variation within the parental state (e.g. the distance travelled or the number of ponds sampled before depositing the tadpole in a pond). (c) Behavioural plasticity may also facilitate expression of parental behaviour in the typically noncaregiving sex (i.e. cross-sexual transfer). (d) All these forms of within-species plasticity may facilitate the evolution of alternative parental care modes between species.

plasticity manifests across scales, its role in adaptation and the evolution of plasticity itself.

PLASTICITY AND PARENTAL CARE

Parental care has arisen repeatedly and independently across animals, imposing fitness consequences on parents and offspring, and laying the groundwork for the evolution of other complex social behaviour (Clutton-Brock, 1991; Royle et al., 2012). Becoming a parent involves profound, often prolonged, changes in behaviour with the potential for individual variation in multiple dimensions, including induction of the parental state, degree of plastic adjustments in care and general parental style. Plasticity in care allows parents to optimize investments for current environmental conditions and offspring needs, to balance trade-offs between current and future reproduction and to negotiate conflict between parents and between parents and offspring (Clutton-Brock, 1991; Royle et al., 2012). Although parental care is generally expressed in adulthood (except in cases of juvenile alloparental care), early life experiences can shape life-long parental behaviour (e.g. Champagne & Meaney, 2001; Gleason & Marler, 2013), and parenting can in turn play an important role in shaping offspring traits (Uller, 2012).

Given that variation in the costs and benefits of parental care across multiple levels has been extensively studied by behavioural ecologists (Royle et al., 2012), the mechanisms that regulate transitions into a parental state, the performance of specific parental behaviours and the links between them are a great place to look for evidence of selective fine-tuning of behaviour and the role of cross-sexual transfer in behavioural evolution. A growing body of empirical studies will help identify generalities, as well as specificities, in the mechanisms mediating parental care at ecological and evolutionary timescales.

Behavioural diversity across poison frogs and other anurans (Delia et al., 2017; Westrick et al., 2022) provides an excellent opportunity to conduct powerful comparative and evolutionary neuroscience studies of the type outlined by recent calls for the development of model clades (Jourjine & Hoekstra, 2021). As noted by West-Eberhard, poison frogs in the family Dendrobatidae are an excellent model clade to investigate mechanisms of plasticity and evolution in parental care owing to remarkable diversity in care mode across closely related species, including maternal, paternal and biparental care modes (Fig. 2; Roland & O'Connell, 2015; West-Eberhard, 2003). Poison frogs lay terrestrial eggs, which they hydrate, clean and defend until hatching, at which point tadpoles are transported 'piggy-back' to bodies of water where they develop and metamorphose (Wells, 2007; Weygoldt, 1986). While the primary caregiving sex varies by species, several species exhibit sex-role plasticity in parental behaviour, with the typically noncaregiving sex occasionally taking over parental duties (Fischer & O'Connell, 2020; Killius & Dugas, 2014; Ringler et al., 2013, 2015; Tumulty et al., 2014). Poison frogs therefore present an exciting group specifically for the study of cross-sexual transfer, as behavioural flexibility *within* species may be a key driver of evolutionary transitions in parental care mode *between* species.

HOW DOES PLASTICITY CONTRIBUTE TO VARIATION AMONG AND WITHIN INDIVIDUALS?

To understand how individual variation in behaviour translates into evolutionary change and elaboration of phenotypes, we first need to understand how mechanisms underlying individual variation produce the behaviours that are screened by selection (Duckworth & Sockman, 2012; McEntire et al., 2022). This requires closer examination of the ways in which mechanisms operate across scales of behavioural expression to modulate or constrain degrees of responsiveness.

Behavioural phenotypes are products of the prevailing environment as well as experiences over the lifetime of the individual. These timescales contribute in a nonmutually exclusive manner to continuous variation among individuals in how often they express a specific behaviour and the degree of flexibility in expression of the behaviour. In essence, cues in the immediate environment 'flip the switch' to activate the behaviour and 'turn the dial' to adjust expression of the behaviour ('activational plasticity' sensu Snell-Rood, 2013, or 'contextual plasticity' sensu Stamps, 2016), while experiences throughout an individual's lifetime tune the sensitivity of the switch and dynamic range of the dial ('developmental plasticity' sensu Hoke et al., 2017; Snell-Rood, 2013). For example, a hatched tadpole may trigger transport behaviour, whereas local habitat features, climatic conditions and previous parental experience may modulate the amount of time parents spend finding an ideal pond for their tadpoles, with variation among individuals in their sensitivity to various cues. Below we break down these different aspects of individual variation in behavioural plasticity and their mechanisms, starting with the impact of the immediate environment.

Behavioural Variation Within Individuals in Different Contexts

To understand how mechanisms contribute to individual variation in parental behaviour, we can begin by considering an isolated bout of parenting. Cues from the environment can alter physiology, neural state and/or gene expression, pushing individuals past their 'threshold' to trigger a discrete change in behaviour, in essence flipping a master switch to induce transition to a parental state (Fig. 3a, b, orange lines). These transitions can happen abruptly or gradually depending on the sensitivity and time course of transducing mechanisms. For example, the brilliant-thighed poison frog, *Allobates femoralis*, rapidly shifts into a parental state and begins to seek water in response to tactile stimulation by a tadpole (Pašukonis et al., 2017), whereas nonparental Japanese quail, *Coturnix japonica*, must be exposed to chicks overnight to enter a parental state and express associated behaviours (de Bruijn et al., 2020; Lopes & de Bruijn, 2021).

Reaction norms are more commonly used to depict activational plasticity within a behavioural state as a function of environmental variation (Fig. 3a, b, blue lines), although the distinction is rarely made apparent. The true shape of this plasticity can be linear or nonlinear depending on the underlying mechanisms (e.g. hormones or gene expression changes) that mediate the response (Sultan & Stearns, 2005). For example, when environmental cues are transduced through hormones, the behavioural response may be linear or dose dependent, with the latter resulting in a step-like response when the hormone passes a threshold, or an inverted-U response curve with low and high concentrations of a hormone corresponding to low expression of behaviour or vice versa

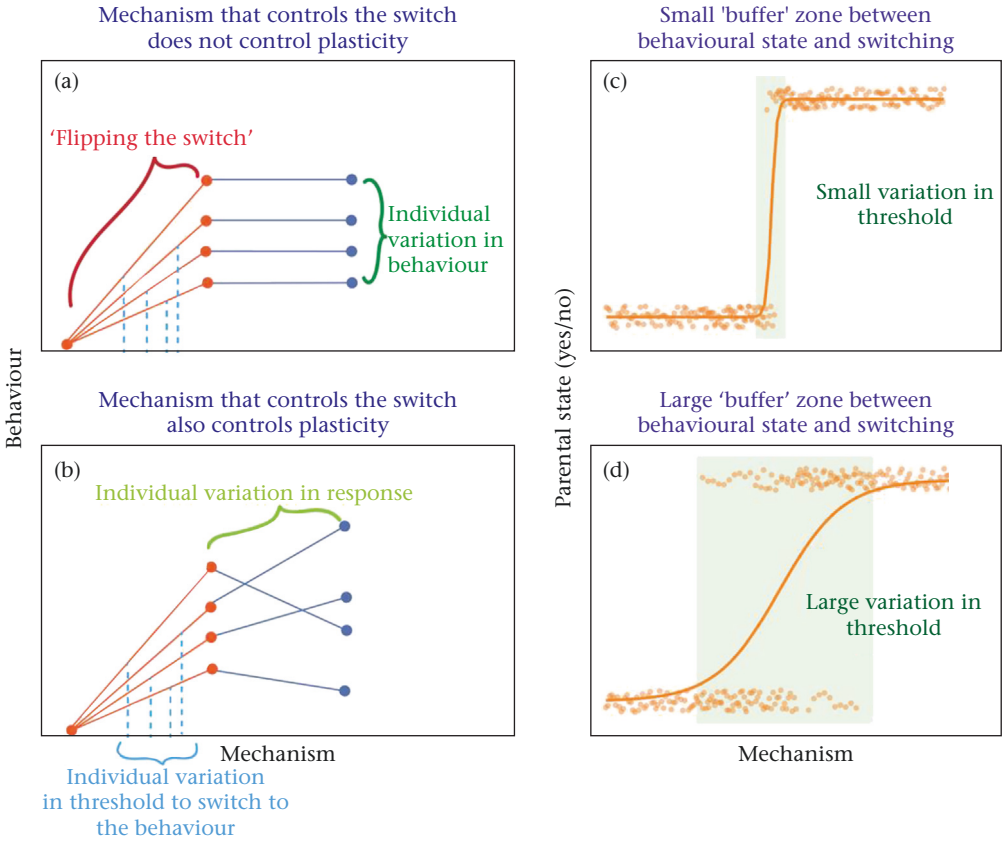

Figure 3. Reaction norms and buffer zones. (a, b) Reaction norms are used to depict changes in behaviour across internal or external conditions or developmental environments. Each line in (a) and (b) depicts one individual's response. Some mechanisms may be involved in (a) the switch (orange lines) to a behaviour or behavioural state but not plastic variation within that state (blue lines), while others (b) may be involved in both the switch and further modulation, which could vary among individuals (as depicted in b) or have a consistent effect among individuals (not pictured). The hypothetical pattern depicted here could also be reversed along the *X* axis; for example, higher concentrations of hormones being involved in the behavioural switch and lower concentrations involved in variation within the state. (c, d) The 'threshold' to switch into a behavioural state may vary within and across individuals. (c) A small 'buffer zone' (green rectangle) allows for rapid switching between behavioural states, whereas (d) a large 'buffer zone' between states may prevent transitory changes from inducing a switch. Again, this is a hypothetical scenario, and the pattern may be reversed along the *X* axis, with higher values of the mechanism of interest 'shutting off' the behaviour.

(Adkins-Regan, 2005; Hau & Goymann, 2015). However, studies often only depict linear effects due to limited experimental groups, contexts or time points. Moreover, it is unclear whether and how the mechanisms underlying discrete switches and continuous behavioural variation are related (Fig. 3a, b). For these reasons, traditional reaction norms may sometimes be inadequate for depicting the true complexity of the relationship between underlying mechanisms and behavioural responses. Whether the same mechanisms that trigger behavioural 'switches' between states are also responsible for continuous behavioural plasticity within those states remains an open question.

Given that parental care is a collection of complex behaviours and some demands of parenthood remain constant across the entire parental period, some physiological and genomic mechanisms implicated in the switch to care likely carry over into the parental state. For example, while some genes implicated in the initial transition to the parental state show no correlation between expression levels and continuous variation within the parental state, others have persistent effects throughout subsequent behavioural transitions and within the parental state (Bell et al., 2016; Benowitz et al., 2019; Bukhari et al., 2019). In the first case, selection may finely tune the switch to parenting without interfering with specific parenting behaviours (Fig. 3a), whereas in the second case, both processes rely on a shared mechanism, which may constrain immediate and evolutionary responses (Fig. 3b; Ketterson et al., 2009; McGlothlin & Ketterson, 2008).

Increased modularity through the evolution of distinct regulatory mechanisms increases complexity but also evolvability (Badyaev & Morrison, 2018; West-Eberhard, 2003) and so may be favoured under a range of circumstances; for example, where subtle modifications in behaviour are desirable without causing dramatic shifts between states. Once animals enter a parental state, it is usually critical to maintain this state even if the original inducing cue (e.g. contact with eggs or offspring) is temporarily absent, as in seabirds that maintain high levels of the nursing hormone prolactin even when separated from their offspring for day-long foraging trips (Vleck & Vleck, 2011). If the response threshold or 'buffer zone' separating a nonparental state from a parental state were narrow, then activational plasticity triggered by small drops in prolactin levels might push an individual back and forth across the switch point of behavioural states (Fig. 3c). Thus, an expansion of this buffer zone could contribute to the stability of a behavioural state despite small fluctuations in the environment and/or in the mechanism that originally pushed an individual across the switch point (Fig. 3d). More empirical studies are needed to test whether the decoupling of the onset mechanisms from the mechanisms required to sustain the behavioural state is facilitated by optimization of the buffer zone or by dampening/increasing the responsiveness of the mechanism.

In summary, if state switches and continuous variation rely on the same mechanisms (Fig. 3b), this may limit plasticity and selective fine-tuning. More studies are needed to determine which switches *between* behavioural states are driven by the same mechanisms as continuous plasticity *within* behavioural states, how much buffering mechanisms over short timescales relate to those that promote consistency of behaviour across longer timescales and how readily traits can be coupled or uncoupled through changes in regulatory architecture. These foundational studies will be critical for understanding within-species patterns before we can draw links to patterns at higher levels of organization; that is, investigate how plasticity within species influences evolution between species.

Contributions of Within-individual Mechanisms to Among-individual Variation

The same mechanisms driving behavioural variation *within* individuals may also extend to variation in behaviour *among* individuals (Lema, 2020; Fig. 3). Both consistent among-individual variation in behaviour (i.e. 'animal personality'; Dingemanse et al., 2010; Stamps & Groothuis, 2010) and among-individual variation in plasticity (i.e. variation in the propensity or extent to which individuals alter their behaviour) are influenced by underlying variation in physiological and genetic mechanisms (Cardoso et al., 2015; Harris & Hofmann, 2014). While many studies addressing the link between among-individual variation and within-individual plasticity approach the topic from a genetic perspective (e.g. Dingemanse et al., 2012), we may also see links in other mechanisms (e.g. hormones, gene expression, neural networks). For example, hormone profiles differ between parental and nonparental poison frogs (Fischer & O'Connell, 2020); however, it is unknown whether this variation between states is also reflected in consistent among-individual variation within the parental state. If baseline variation and plasticity are free to evolve independently, this may facilitate fine-tuning of mechanisms to a specific context (e.g. parental care) without disrupting other behaviours.

Both among-individual variation in behaviour and behavioural plasticity may be established early in life through development by plasticity shaping variation in the machinery underlying complex traits, such as hormone receptor density, neurogenesis and gene expression (Beldade et al., 2011; Caldji et al., 2011; Champagne, 2013; Dingemanse et al., 2010; Dingemanse & Wolf, 2013; Loi et al., 2014; Mitchell & Houslay, 2021; Trillmich et al., 2018; Westneat et al., 2011). For instance, rat pups who are groomed more have higher expression of glucocorticoid receptors in the hippocampus, are less fearful as adults and perform more grooming of their own pups compared to pups groomed less (Francis et al., 1999; Liu et al., 1997). Early life factors shaping the distribution and density of hormone receptors can modulate the release of and sensitivity to hormones later in life, which can in turn result in variation in behavioural plasticity between individuals (e.g. Bairos-Novak et al., 2018; Glover et al., 2010; Love & Williams, 2008; Meaney, 2001).

Repetitive events throughout the life of an individual (e.g. mating or parental experience) can further 'fine-tune' the responsiveness of the neuroendocrine system through iterative developmental plasticity, where repeated cues induce repeated modifications (Foster et al., 2015; Stolzenberg & Mayer, 2019). For example, in common terns, *Sterna hirundo*, reproductive success increases with age, and individuals with more breeding experience have higher levels of prolactin during the breeding and parental care period than younger, inexperienced birds (Riechert et al., 2012). Notably, this pattern of increased prolactin with age holds within and among individual terns (Riechert et al., 2012). Further understanding the relationship between mechanisms of developmental and activational plasticity will help explain limitations of plasticity and how individuals maintain consistent differences (Duckworth, 2015).

Incorporating more mechanisms into our study of individual variation in behaviour will also allow us to more rigorously test the alternatives that within-group differences and among-group differences rely on the same, versus distinct, mechanisms (Adkins-Regan, 2005; Niemelä & Dingemanse, 2018; Fig. 1). Additional empirical studies are needed to disentangle currently equivocal results. For example, there is still conflicting empirical evidence on the effects of testosterone on parental behaviour in birds (reviewed in Lynn, 2008). Many studies have shown that testosterone

implants suppress parental behaviour in male birds (e.g. dark-eyed juncos, *Junco hyemalis*: Ketterson et al., 1992); however, other studies examining natural variation in testosterone show no relationship between testosterone and parental behaviour (e.g. black redstarts, *Phoenicurus ochruros*: Villavicencio et al., 2014). To test this discrepancy, Goymann and Flores Dávila (2017) used a more individual-based approach to testosterone manipulation in black redstarts and found that short-term increases in testosterone within an individual's typical range of testosterone do in fact supress paternal behaviour. Similarly, testosterone is known to promote the expression of courtship behaviour and aggression at an individual level (Soma, 2006; Wingfield et al., 1987). Yet, looking across species, with a sample of small, temperate zone, socially monogamous songbirds, we find substantial differences in the precise regulatory relationship between testosterone and territorial aggression (Hau & Goymann, 2015).

Additionally, expanding mechanistic studies to look within and across individuals could reveal whether correlated selection on mechanisms facilitates or constrains behavioural plasticity and the evolution of behaviour. Variation within individuals (e.g. plasticity in response to age or condition) can obscure relationships between underlying mechanisms and behaviour among individuals. It is therefore critical to consider the contribution of plasticity within individuals when looking for patterns across a group or population (Fig. 1; Adkins-Regan, 2005; Hau & Goymann, 2015; Malkoc et al., 2022). Differences in developmental trajectories between sexes further stratify relationships between mechanisms and behaviour within and among individuals, and variation at each of these levels may ultimately vary across species.

HOW DOES PLASTICITY CONTRIBUTE TO VARIATION BETWEEN SEXES AND SPECIES?

In addition to differences among individuals of the same type, parental care and plasticity in parental behaviour may be expressed differently depending on age, dominance class, reproductive strategy and sex. In this section, we explore how mechanistic studies can test the evolutionary links between behavioural variation measured at the individual, sex and population scale.

Flexible Sex Reversal of Parental Behaviours

Parental care provides striking examples of sex differences in behaviour, as care is often performed disproportionately or exclusively by one sex, and sexes can play distinct roles in care (e.g. provisioning offspring versus defending the nest; Henshaw et al., 2019). Sex of the caring parent is the primary way we classify natural diversity in parental care systems, but plasticity in parental care can blur the lines along which we typically distinguish maternal versus paternal care. Furthermore, males and females can also be differentially plastic, both in terms of their sensitivity to environmental cues as well as their opportunity to adjust behaviour once in a parenting state (Moss & Moore, 2021; Ringler et al., 2016; Rossmanith et al., 2009; Smiseth et al., 2005). For example, stressful environmental conditions can reveal hidden plasticity in sex roles in systems with biparental care, as in birds that respond to extreme weather with increases in male care, resulting in more egalitarian division of labour between the sexes (AlRashidi et al., 2010; Vincze et al., 2017). This plasticity lays the foundation for cross-sexual transfer of behaviour.

Most sex differences in behaviour are actively maintained by underlying neural, physiological and molecular mechanisms (de Vries, 2004; Dulac & Kimchi, 2007; Gegenhuber & Tollkuhn, 2020; Kimchi et al., 2007; Leitner & Ben-Shahar, 2020). Therefore, rather than think of cross-sexual transfer as the creation of a brand-new behavioural repertoire, it is more parsimonious to imagine a different behavioural repertoire emerging due to the activation of typically quiescent underlying mechanisms (Fig. 4; Adkins-Regan, 2005; West-Eberhard, 2003). The capacity for plasticity in parental roles in many species implies that some individuals of the typically noncaregiving sex are operating near enough to the switch point between states that an environmental change (e.g. loss of the primary caregiver) may push them beyond the limits of their mechanistic buffer zone and trigger rapid changes in behaviour (Fig. 4a–c; Hoke et al., 2019; Pfennig, 2021; West-Eberhard, 2003). Evidence for this 'priming' effect can be found in mechanistic investigations that include noncaregiving partners alongside primary caregivers. For example, parents who show no involvement in egg brooding or pregnancy may nevertheless take on hormonal profiles resembling those of their partner with extended contact (Brown et al., 1995; Gubernick & Nelson, 1989; Reburn & Wynne-Edwards, 1999; Storey et al., 2000; Van Roo, 2004). Such internal state matching has also been shown in a species of poison frog with male-only care, in which typically noncaregiving females show hormonal and brain gene expression changes that parallel those of their actively caregiving male mates (Fischer & O'Connell, 2020). Manipulations aimed at identifying the mechanisms responsible for the activation of behaviour will cast light on how switch points between 'female-like' and 'male-like' expression may be surpassed with such apparent spontaneity.

Once in a parental state, males and females may also differ in their continuous behavioural responses to environmental cues. At a behavioural level, males and females may express care in different functional contexts and may be sensitized to different stimuli and/or experience different trade-offs (e.g. an intruding male may represent a threat to a male parent but an opportunity to a female parent). At a mechanistic level, a range of network configurations has the potential to produce similar phenotypes (Fischer et al., 2016), such that the precise neural (Kohl et al., 2018) and gene network (Bendesky et al., 2017) configurations that correspond to a particular phenotypic output may differ between the sexes (Fig. 4d–f). For example, in a quantitative genetic study of parental care in mice (*Peromyscus* spp.) Bendesky et al. (2017) identified most genomic regions as having sex-specific effects on behaviour, even though parental behaviours themselves are similar between the sexes. Ultimately, we must understand the extent to which mechanisms of plasticity are shared or distinct between the sexes to predict how selection differentially fine-tunes maternal versus paternal behaviour and evolutionary transitions between care strategies.

Finally, individuals may respond differently to conditions that are permissive for cross-sexual transfer. Sex-specific developmental trajectories that inhibit expression of parenting traits may allow for cryptic variation to accumulate at various levels responsible for modulating trait form and function. For instance, individual variation in baseline hormone levels or hormonal rhythms during time periods leading up to care may tune neural circuits such that the circuits of some individuals may be closer to the threshold for entering the parental state (Hoke et al., 2019; Fig. 4a). Moreover, variation early in development when network connections are forming may influence the fidelity with which females are able to reproduce functional male-like network states and behaviour and vice versa (Fig. 4d). For example, genetic female rats treated with androgens during critical periods in development present masculinized behavioural repertoires as adults (Goy & McEwen, 1980). If immediate and developmental mechanisms contributing to this individual variation are correlated and the inducing environment is recurrent, selection may rapidly sort among variants and enhance the sensitization of successful genotypes to relevant external and internal stimuli (West-Eberhard,

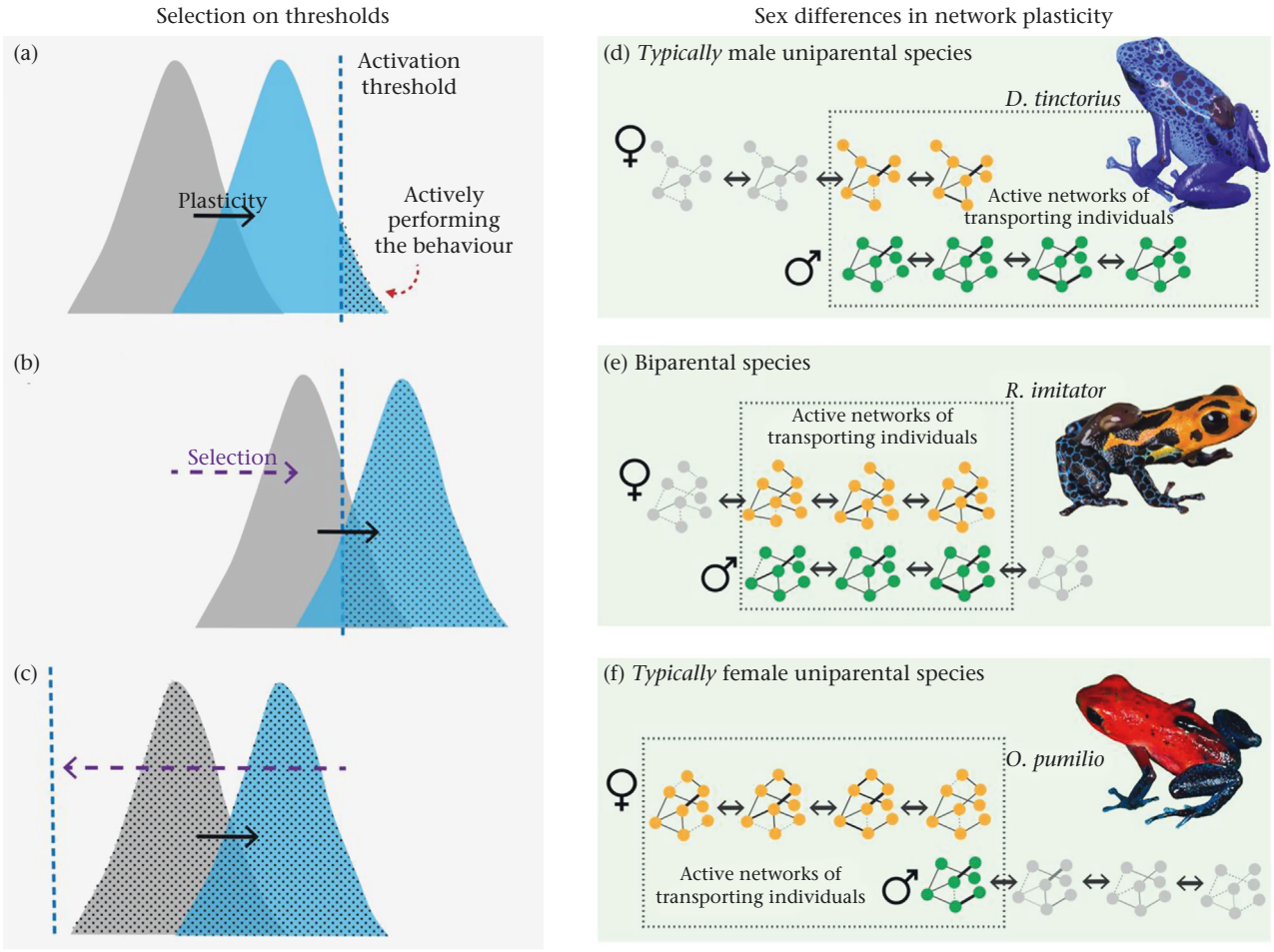

Figure 4. Selective fine-tuning of switch points and regulatory networks underlying parental behaviour across sexes and species. (a, b, c) Individual variation (grey histogram) in baseline proximity to the population activation threshold (blue dotted line) determines the proportion of the population that will express a given behaviour under inducing environmental conditions (blue histogram). In (a), the population is under selection to suppress the behaviour under many conditions, such that even in inducing conditions (black arrow), the behaviour is performed only in rare individuals (dotted area). In (b), selection on individual baseline variation (purple dashed arrow) has shifted the population mean closer to the activation threshold, such that inducing conditions trigger the behaviour in many individuals (i.e. plasticity is genetically accommodated). In (c), selection on the switch point itself has lowered the activation threshold (purple dashed arrow), such that the original inducing cue (black arrow) is no longer necessary to elicit the behaviour (i.e. the behaviour is genetically assimilated). (d, e, f) Individual variation in network states corresponding to inactive (greyscale) and active (coloured) behavioural states, in this example, tadpole transport. Females (orange) and males (green) may show sex-specific configurations and plasticity of network states (i.e. bidirectional arrows indicate transitions in network state) owing to dimorphic developmental and physiological influences. Hypothetical patterns are depicted for three species of poison frog that differ in parental care mode: (d) in a paternal species, tadpole transport is performed almost exclusively by males, but females occasionally transport; active network configurations may be achieved by only a few females; (e) in a biparental species, males typically perform tadpole transport, but females readily take over; active network configurations are achieved by most females; (f) in a maternal species, female-specific network configurations have been selectively fine-tuned to optimize behavioural performance across variable environments, whereas males rarely achieve active network configurations.

2003). These observations highlight why we need studies linking individual variation to cross-sexual transfer.

Cross-sexual Transfer and the Evolutionary Diversification of Parental Care Modes

If plasticity can promote the occasional transfer of complex traits between the sexes, then selection on this plasticity may, over evolutionary time, help explain diverse patterns of care across species. As with the relationship between variation measured within and among individuals and sexes, it is often assumed that differences *between* species arise from selection on physiological, neural and molecular mechanisms that produce variation *within* species (as in Fig. 1b).

Radiations involving the diversification of parental care are well poised to address these gaps because caregiving systems of closely related species are often characterized by differences in plasticity, including who is expressing care and under what conditions. Different lineages represent distinct historical points along a dynamic continuum of evolving plasticity, where selection may differentially tune underlying mechanisms to accommodate distinct contexts for expression (Potticary & Duckworth, 2021). For instance, population and species level comparative work in voles (genus *Microtus*) has uncovered tremendous variation in the extent of male and female involvement in care (McGraw & Young, 2010), as have comparisons of closely related populations of a biparental shorebird (genus *Charadrius*; Vincze et al., 2013) and crosses between *Peromyscus* mouse species with distinct social systems (Bendesky et al., 2017).

As discussed above, conditions conducive to flexible sex reversal of parental behaviour may reveal cryptic variation at the individual level, both in the ability to overcome thresholds for transitioning between states (Fig. 4a–c) as well as the capacity to generate functional network configurations that trigger a change in

behaviour (Fig. 4d–f). When the inducing environment is recurrent, selection will favour genotypes that more readily produce parental behaviour. Returning to poison frogs, if we assume that the priming of physiological and neurogenomic pathways plays a role in the capacity for flexible sex reversal of tadpole transport behaviour, we may predict that the transition from male-only care to biparental care occurs via selective refinement of female plasticity. A recent study demonstrated just this: while females of a species with male-only care (*Dendrobates tinctorius*) and biparental care (*Ranitomeya imitator*) do not typically transport tadpoles, females of the biparental species show more male-like patterns of neural induction while fathers are caring than do females of the species with male-only care (Fischer et al., 2019). This suggests that the sensitivity of female neural networks may be fine-tuned during evolutionary transitions in care mode, thereby increasing the likelihood that a sudden (social) environmental change can trigger compensatory behaviour, and ultimately allowing behaviour to become accommodated at the genetic level as the proportion of females that spontaneously express parental behaviour increases (Fig. 4b; Potticary & Duckworth, 2021; Snell-Rood, 2013; West-Eberhard, 2003).

A final pattern that may emerge from occasional sex reversal of parental behaviour is the complete transfer of caregiving duties between the sexes. Apart from mammals, where female care is obligate due to lactation, transitions from female-only to male-only care and vice versa are present in almost every major lineage (Klug et al., 2013; Royle et al., 2012) and may even be more common than previously thought. For example, a comprehensive re-examination of the natural history of 40 species of Neotropical glass frogs (Centrolenidae) showed that extended male-only care, previously thought to arise exclusively from an ancestral state of no-care, in fact evolved two to three times from brief periods of female-only care (Delia et al., 2017). Although it is difficult to test whether the process of obligate care changing hands involves a stage with facultative care (i.e. asymmetric biparental care), this evolutionary sequence has been proposed to explain the stable transfer of care from males to females in poison frogs (Summers & Earn, 1999; West-Eberhard, 2003). Under such a scenario, females that previously transported tadpoles only in response to rare events (e.g. mate loss) should instead couple this behaviour to a more ubiquitous cue (e.g. offspring need) and potentially expand their buffer zone to inhibit premature exit out of the parental state. In either case, the threshold for activation is shifted, and therefore the ancestral environmental trigger is no longer necessary to elicit the behaviour (the behaviour has been genetically assimilated; Lande, 2009; Pfennig, 2021; West-Eberhard, 2003; Fig. 4c). This process may be accompanied by stabilizing connections within the network to reduce phenotypic variability within the parenting state (Fig. 4f). Ultimately, more mechanistic investigations across taxa are needed to understand how differential fine-tuning of mechanisms contributes to shared versus distinct patterns of parental care across lineages.

Conclusions

An outstanding challenge in integrative, multilevel discussions of plasticity is how to connect relationships between complex phenotypes and underlying mechanisms across multiple levels. Reaction norms are commonly used to depict plasticity, but they have some limitations, and we suspect that their use in multiple contexts without clear differentiation has contributed to imprecision in distinguishing among the different levels at which behavioural plasticity can be characterized (Fig. 5a, b). We borrow from a visual mapping approach applied by others (Hoke et al., 2019; McEntire et al., 2022; Oster & Alberch, 1982) to demonstrate how the levels we discuss in this paper connect to one another and to underlying mechanisms (Fig. 5). While plasticity has been extensively investigated within each level of this framework, empirical studies that examine patterns of plasticity across multiple levels are needed to further our understanding of behavioural plasticity and its evolution.

Plasticity within individuals is a fundamental feature of behaviour that allows individuals to adjust to different environmental conditions (Fig. 5a). Variation between individuals takes multiple forms, arising from the fact that individuals can vary in how often they express a behaviour, how much they express a behaviour and the degree of plasticity they display in the behaviour (Fig. 5b). Whether these different axes of individual variation rely on shared or distinct mechanisms is an outstanding question with important consequences for our understanding of how

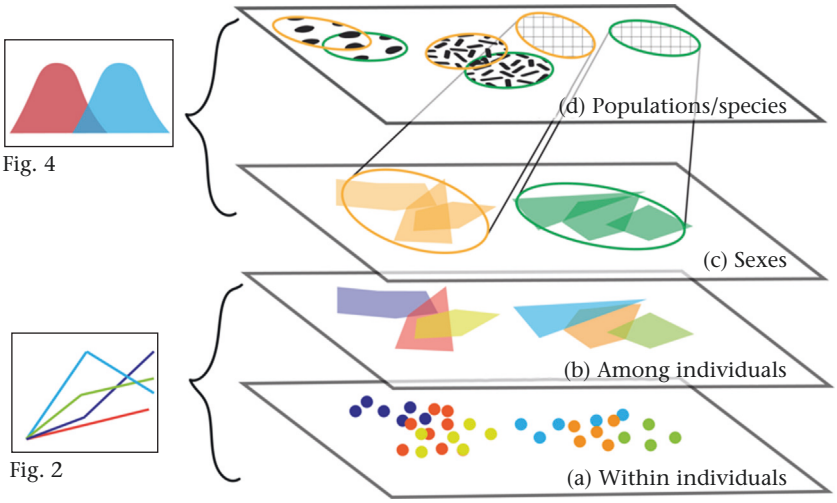

Figure 5. Behavioural plasticity and variation in plasticity permeates across multiple levels of biological organization. We depict multiple stacked levels to pull the thread of behavioural plasticity across multiple scales and show how these levels of biological organization are intrinsically linked. Behavioural plasticity (a) within individuals shapes the variation in phenotypic space occupied (b) among individuals. Across both (a) and (b), we can use a reaction norm approach to measure variation and plasticity (see Fig. 2). Developmental differences between (c) sexes may drive some similarities among individuals. This overlap or lack thereof between sexes can differ (d) among populations and species. The phenotypic space of the different sexes may overlap to varying degrees as variation within and among individuals is transduced across levels (see Fig. 4).

underlying mechanisms mediate continuous behavioural variation versus discrete behavioural state changes and whether reliance on shared mechanisms leads to immediate and evolutionary trade-offs.

Plasticity between sexes lies at the intersection of individual, population and species level patterns (Fig. 5c, d). As males and females of the same species often exhibit marked behavioural differences despite largely shared genomes and neural networks, this level of organization provides a particularly intriguing entry point for studies addressing how underlying mechanisms buffer versus facilitate behavioural change. This form of plasticity is also particularly interesting in the context of parental behaviour, where it has both immediate consequences for offspring survival and likely serves as a substrate for the evolution of alternative parental care modes. Moving forward, integration across levels will shed light on whether mechanisms of within-individual plasticity and among-individual variation are shared, how combinations of shared and distinct mechanisms give rise to differential plasticity between sexes, and whether and how mechanisms mediating plasticity are co-opted for behavioural evolution among species.

After decades of research, the role of plasticity in evolution remains a focus of theoretical and empirical work. Renewed interest in this topic has come alongside the genomic revolution of the last two decades, which has enabled genomic approaches in a growing number of species, including those particularly well suited for probing the mechanisms underlying phenotypic plasticity, the relationship between plasticity and adaptation, and the evolution of plasticity itself. These studies have confirmed that relationships between plasticity in underlying mechanisms and organismal level traits are varied, complex and contingent on the level of analysis. Standing on the shoulders of giants like Susan Foster and others, and linking across traditionally distinct fields of study, we have attempted to illustrate how plasticity manifests across levels of organization and timescales and how plasticity at proximate levels may shift from buffering to reshaping organismal level phenotypes.

Our goal here was to explore how behavioural plasticity is regulated across levels of comparison and how this influences patterns of plasticity, behavioural evolution and the evolution of plasticity itself. We used cross-sexual transfer of parental behaviour as a specific example of how plasticity may translate intraspecific behavioural variation within and among individuals to adaptive variation between sexes and species. We included specific examples to highlight how mechanistic thinking can be applied to patterns of plasticity within and among individuals, sexes and species, considering how the mechanisms of plasticity can become targets for selection in each case. These concepts remain complex, and we emphasize there is no single entry point for addressing the role of phenotypic plasticity in adaptation. Nevertheless, we feel that multilevel thinking is applicable to behaviours and phenotypic traits more generally, and hope that our discussion here will inspire ongoing integration of mechanisms into studies of the evolution of plasticity.

Author Contributions

Sarah E. Westrick: conceptualization, visualization, writing – original draft, writing – review & editing. **Jeanette B. Moss:** conceptualization, visualization, writing – original draft, writing – review & editing. **Eva K. Fischer:** conceptualization, visualization, writing – original draft, writing – review & editing.

Data Availability

No data were used for the research described in the article.

Declaration of Interest

None.

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