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Correlated behavioural plasticities: insights from plasticity evolution, the integrated phenotype and behavioural syndromes

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Integrated phenotypes, that is, correlated suites of traits, can impact both evolutionary and ecological processes. Similarly, phenotypic plasticity, or the ability of one genotype to generate multiple phenotypes, can act as both a facilitator and constraint on evolutionary processes. While there has been an increasing focus on correlated behavioural means (i.e. behavioural syndromes), less attention has been paid to how plasticity in different behavioural traits may be correlated. Such correlated behavioural plasticities are likely to affect evolution and ecology, although possibly in different ways. Here, we review key insights from three research fields, behavioural syndromes, phenotypic plasticity and integrated phenotypes to provide a conceptual framework to understand why, how and when plasticities of different behavioural traits may become correlated. In particular, the conditions under which plasticity and behavioural syndromes are predicted to be important are also where correlated behavioural plasticities are likely to have the strongest impacts. In this review, we define correlated behavioural plasticities, summarize the conditions that are likely to give rise to them and highlight testable predictions in an effort to spark targeted research into this important phenomenon. We also provide a worked example to highlight how studying correlated plasticity can yield important new insights.

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The study of consistent individual differences in behaviour is a booming topic of interest. These individual differences have important effects on both evolution and ecology (Dingemanse & Réale, 2005; Sih et al., 2004, 2020). Importantly, even though individuals consistently differ in their behaviour, this does not imply that behavioural expression is completely rigid. Organisms can, and do, respond to a variety of environmental conditions such as changes in temperature or social status, and thus exhibit plasticity in their behaviour, even if their average behaviour may not differ from that of other individuals (Fig. 1a) (West-Eberhard, 2003). Importantly, responding to such environmental changes often requires coordinated change across several traits, a phenomenon that has been described as multivariate phenotypic plasticity or plasticity integration (Pigliucci, 2003; Westneat et al., 2019). While the integration of plasticity across physiological and/or morphological traits been a topic of interest for some time (Ellers & Liefting, 2015; Schlichting, 1989), especially in plants and insects, behaviour-specific empirical work on how plasticity in different behavioural traits may be related has not enjoyed as much attention. A focus on correlated plastic behaviours specifically could have important implications for ecology and evolution. Understanding the adaptive significance of these correlations might improve our predictions for animals' responses to changing environmental conditions.

There has been considerable empirical work investigating patterns of variation in individual average behaviour (i.e. 'animal personalities' or 'behavioural types') and correlations among average behaviour (i.e. 'behavioural syndromes'; Dingemanse et al., 2004; Réale et al., 2007; Sih et al., 2004). However, variation in average behaviour, that is, the repeatability of behaviour, is typically only about 0.37 and the correlation among average behaviours is about 0.20 (Bell et al., 2009; Garamszegi et al., 2012). This means that far more variation exists within individuals than among them. Indeed, there is a rich literature now investigating plasticity in single behavioural traits (e.g. Brass et al., 2021; Dingemanse, Kazem, et al., 2010; Niemelä & Dingemanse, 2018; Stamps, 2016). However, research on how plasticity in several different behaviours may be correlated has been less explored. There are two reasons that may explain this lack of empirical work. First, there has not been a consolidated summary of the key overlaps and predictions between animal behaviour, plasticity and integrated phenotypes. Second, prior to recent advances in automated behavioural coding
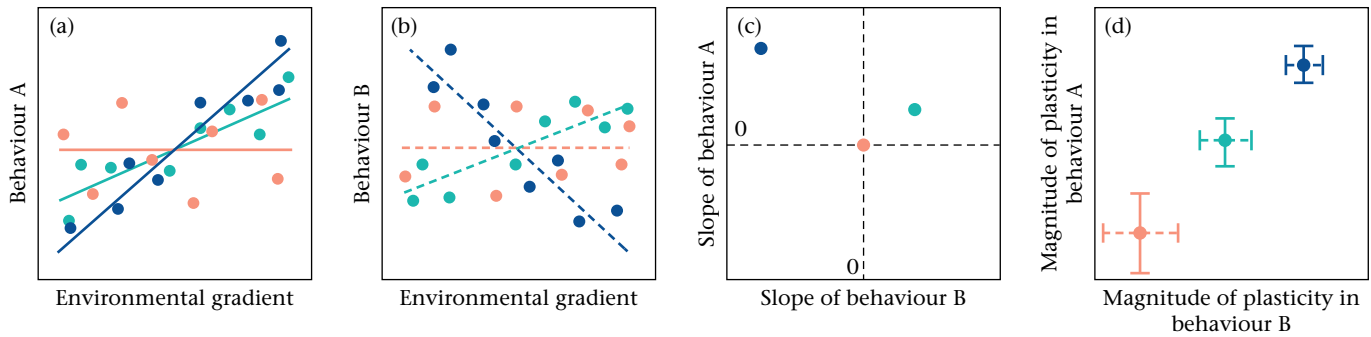
Figure 1. The behavioural responses of three individuals across an environmental gradient, such as temperature or predator prevalence. The pink points represent an individual that does not exhibit behavioural plasticity in behaviour A or B ((a, b): slope = 0), but does exhibit more stochasticity around that slope (error bars in (c)). The dark blue points indicate another individual that exhibits high plasticity in both behaviour A and behaviour B, but the direction of the slope is different ((a) slope >> 0; (b) slope << 0). The teal individual has a positive plastic response in both behaviours A and B, although its degree of plasticity is lower than that of the dark blue individual ((a, b): teal slope > 0). All three individuals have the same mean expression of behaviours A and B. There is not an obvious pattern of correlation between slope direction (c). However, across all three individuals, there is a correlation between the magnitude of plasticity in behaviours A and B (d).

software and statistical analysis (Jolles, 2020; Stoffel et al., 2017; Walter & Couzin, 2021), the sample sizes needed to examine plasticity in multiple behaviours were prohibitively large and the statistical methods required were highly specialized (Dingemanse, Dochtermann, et al., 2010; O'Dea et al., 2021; Pigliucci, 2003). Here, this review seeks to fill this gap by summarizing the essential insights from each field, identifying important and promising hypotheses and highlighting experimental systems and techniques that can help advance the study of correlated behavioural plasticities.

WHAT DO WE MEAN BY 'CORRELATED BEHAVIOURAL PLASTICITIES'?

As a discipline-spanning concept, plasticity has been defined several ways, with subtle and sometimes dramatic distinctions that are important to the respective field (see Pfennig, 2021 for a broad overview). In this review, we elect to stick to a broad definition: plasticity is the change in an individual's phenotype as a function of environmental (external or internal) variation (for a thorough overview, see Kelly et al., 2012; Stamps & Biro, 2016). We focus primarily on reversible plasticity as most behaviours can be repeatedly expressed and can change throughout the lifetime of an individual, although we believe that similar conclusions can be drawn about developmental plasticity. Some traits can exhibit irreversible or developmental plasticity, where expression is set at some point early in life; however, this is not typical of behavioural traits. While some behaviours may be expressed as discrete variation (e.g. alternative mating tactics), we generally focus on behavioural traits that exhibit continuous variation. For example, crayfish plastically increase their expression of 'boldness' behaviours with increases in temperature (Ferderer et al., 2022). Such changes in behaviour can be described using a reaction norm (Fig. 1). Here, we distinguish plasticity from other forms of within-individual behavioural change such as 'predictability' (O'Dea et al., 2021) or 'intraindividual variability' (Stamps et al., 2012), which describe the level of stochasticity in individual behaviour over repeated measurements. Unlike plasticity, stochasticity may not be a direct response to environmental variation; that is, it does not predictably respond to (measured) environmental cues. Within the reaction norm framework, this means we will focus on the slope of an individual's reaction norm rather than on how tightly its behaviour is distributed around that slope. We acknowledge that the amount of variation around a reaction norm may also be important and should be studied using the appropriate statistical methods (for further

discussion of stochasticity, see O'Dea et al., 2021). For example, individuals may exhibit higher levels of intraindividual variation in behaviour under predation risk, possibly to be less predictable and better evade predators (Briffa, 2013).

The reaction norm approach is rapidly becoming standard in the field of animal behaviour as it can characterize many aspects of individual behavioural variation simultaneously (Dingemanse, Kazem, et al., 2010). For example, Jolles et al. (2019) found that individual stickleback's (*Gasterosteus aculeatus*) average behaviour predicted their plasticity in behaviour: individuals that were on average less exploratory (i.e. lower intercept), showed greater plasticity (i.e. steeper slope) in that behaviour over time. Westneat et al. (2013) used the reaction norm approach to investigate how female red-winged blackbirds, *Agelaius phoeniceus*, adjust their parental foraging behaviour in the face of several environmental gradients, allowing them to generate several hypotheses about how these birds may be responding to nestling needs and local social interactions. The next step is to expand the concept of reaction norms into a more multivariate world to examine how plasticity in multiple behavioural traits may be related to each other within individuals and across populations (i.e. 'plasticity syndromes'; O'Dea et al., 2021; Westneat et al., 2019). Here, we focus on correlations in slope magnitudes as the direction of slopes is often arbitrarily determined through study design (e.g. lower values of latency to emerge from a refuge and higher values of area explored can both indicate greater propensity to engage in 'risky' behaviour). The core idea is that the slope of an individual's reaction norm in one behaviour may predict the slope of its reaction norm in another behaviour (Fig. 1d). In other words, are behavioural plasticities correlated?

There is reason to believe that an individual that exhibits considerable plasticity in one behavioural trait may also exhibit plasticity in another behavioural trait. There is already a large body of literature on correlated plastic physiological and morphological phenotypes and their evolutionary consequences (Bourdeau et al., 2015; Faulkes & Bennett, 2013; Handelsman et al., 2014; McGlothlin & Ketterson, 2007; Schlichting, 1989). For example, anuran tadpoles have long been models for trait plasticity, so much so that Hossie et al. (2016) conducted a meta-analysis of their plasticity in behavioural and morphological responses to predation threats. Using the extensive empirical literature on tadpoles, they tested whether behavioural and morphological plastic responses were consistent across families. They explicitly examined the relationship of reaction norms to determine the relationship among trait plasticities. They found that behavioural and

morphological reaction norms can be expressed independently of each other but were generally positively correlated (i.e. greater plasticity in one trait predicted greater plasticity in another). This indicates that there is not a trade-off between investing in one strategy over the other, which could be enforced through mechanistic trade-offs. Rather, this indicates that deploying multiple independent antipredator responses (e.g. behavioural and morphological responses) is more optimal than relying on a single response.

Investigating how (or whether) patterns of correlated plasticities change across contexts may help reveal insights into the mechanisms linking traits and the selection pressures generating those correlations. For example, in animals that are predated by gape-limited predators, threat is highest when the animal is young and small, so we may expect to see the tightest correlations in plasticities in antipredator traits in juveniles. This could potentially suggest that these traits are mechanistically linked or linked through correlational selection pressures. These alternatives could be investigated by comparing patterns of correlated plasticity later in life: if the integration relaxes after the animal has grown enough to escape the threat of predation, then mechanistic constraints may not be the drivers of the correlated plasticities. Investigating differences in patterns of correlated plasticities can allow us to generate hypotheses about the selection pressures generating those relationships. For example, a classic study by Berg (1960) found much tighter correlations among suites of morphological traits in some flowering plant species compared to others. Importantly, species that were pollinated by insects showed the tightest integration, which led Berg to hypothesize that signalling to pollinators was a critical driving force in the flowering phenotypes of these plants.

THE IMPORTANCE OF CORRELATED BEHAVIOURAL PLASTICITIES FOR BEHAVIOUR, EVOLUTION AND ECOLOGY

Correlated behavioural plasticities may have important consequences for animal behaviour, ecology and evolution. Predicting whether and how these correlations change is especially important in the face of climate change and human-mediated environmental change. If the field of animal behaviour is to comprehensively understand how animals respond to their environments and the consequences this has for their continued evolution, we need to move beyond exploring single reaction norms and mean behaviours; we need to examine how behavioural plasticities, specifically, are correlated. Here we outline three implications of this type of behavioural variation. First, similar to predictions made about the role of phenotypic plasticity and behavioural syndromes in future evolution, correlated behavioural plasticities may facilitate or constrain adaptive change in populations. These correlations may play as significant a role as behavioural syndromes but have received considerably less focus in the field of animal behaviour. Second, the presence of correlated behavioural plasticities also has the potential to explain behavioural syndromes themselves. Then, finally, correlated behavioural plasticity may also provide better insight into the relationships between behaviours and other physiological 'state' variables (defined in more detail below), which do not appear to be related when looking at mean behaviours alone (Laskowski, Chang, et al., 2022). The patterns observed may generate testable hypotheses for how state and behavioural plasticity may be related.
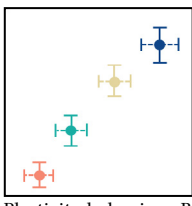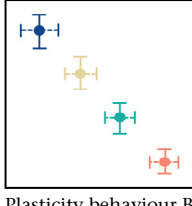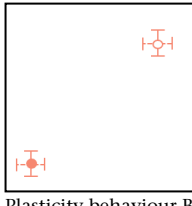
Plasticity is predicted to affect adaptive change in populations in several different ways (Paenke et al., 2007). For example, plasticity can allow populations to persist while evolution 'catches up' with rapid environmental changes (Diamond & Martin, 2021). Plasticity can also expose previously unexpressed phenotypes to selection,

eventually leading to the canalization of the new phenotypes through genetic accommodation (Levis & Pfennig, 2016). Alternatively, plasticity can constrain evolution by breaking the relationship between fitness and heritable genetic variation (Paenke et al., 2007). Behavioural syndromes are also predicted to have similar dichotomous effects on future evolution. Behavioural syndromes are correlations among individuals in the average behaviours they express; for example, the most aggressive individuals also exhibit the most risk-prone behaviour. Among-individual behavioural correlations could facilitate evolution if selection acts in the same direction as the correlation. For example, selection might favour matching (either high or low) expression of both aggression and risky behaviours (e.g. Bell & Sih, 2007). However, if selection acts orthogonally to the direction of the correlation among behaviours, then behavioural syndromes might constrain the speed with which a population can adapt (Dochtermann & Dingemanse, 2013).

The effects of plasticity and among-individual variation in average behaviour on future evolution can be extended to correlated behavioural plasticities. First, plasticity in whole suites of behaviours might better allow animals to cope with complex, rapidly changing environments (Sih et al., 2011; Westneat et al., 2019). Just as the environment can vary in multiple dimensions, such as temperature or social context, animals have several behaviours at their disposal to plastically respond to one or more changes in their environment. Because many environmental variables covary (e.g. daylength and temperature), suites of plastic behaviours are likely to covary in response. For example, in response to lengthening photoperiod indicating spring, male birds may change their dietary preferences, become more aggressive towards conspecific males and begin courtship behaviours such as singing. If plasticity in these behaviours is not correlated, then the male may suffer decreased fitness by failing to alter one or more of these behaviours. A key question is whether plasticity in these behaviours can be initiated from a single cue (e.g. changes in daylength induce plasticity in both dietary preferences and aggression) or whether multiple cues are necessary (e.g. changes in daylength and resource availability are both necessary to initiate changes in dietary preferences and aggression) or whether each trait responds independently to different cues (e.g. dietary plasticity responds to resource availability whereas aggression responds to daylength). It may also be that plasticity in one trait can be the trigger for plasticity in other traits. In this example, if males change their dietary preferences in response to environmental cues, then the increase (or decrease) in resource acquisition may be the trigger to then adjust their aggressive singing efforts. Thus, correlated behavioural plasticities are likely important in scenarios where there are environmental changes in multiple variables at once.

Interestingly, correlated behavioural plasticities may explain the emergence of behavioural syndromes themselves. One of the key predictions of plasticity-led evolution is that the rate and magnitude of evolutionary change should be positively associated with the frequency of an expressed phenotype in a population (Levis & Pfennig, 2016). In other words, the more frequently a plastic trait is expressed, the more opportunities it has for being shaped by natural selection, thus leading to more rapid canalization of a novel phenotype. The plastic expression of multiple phenotypes in conjunction, either because they are controlled by a similar mechanism or respond to the same cue, could be viewed as a behavioural syndrome in the making. If their co-occurrence is adaptive and frequent, then they are more likely to become canalized or linked together, and thus become a syndrome. Importantly, this could explain why we see variability in syndromes across populations (Levis & Pfennig, 2019). For example, exposure to certain environmental conditions has been shown to alter patterns of individual behavioural variation. Guppies exposed to novel

Table 1
Key patterns of correlated behavioural plasticities and predictions about when such patterns might occur

Correlation	Predictions	Systems	Questions
Positive correlations among the magnitudes of two behavioural plasticities	This pattern of correlation is predicted to persist where the coordinated expression of these two traits is important for fitness, or where plasticity in one trait facilitates plasticity in another	Important in systems where communication is part of sociality or sexual displays or even antipredator displays	What are the main drivers of these correlations (e.g. honest signalling or runaway selection in mating systems)? Is inter- or intraspecific signalling more dependent on correlated plastic behaviours?
Negative correlation among the magnitudes of two behavioural plasticities	This pattern is most likely present in systems where there are significant trade-offs or costs to expressing plasticity	Investigating systems with described specialist/generalist phenotypes or alternative modes of reproduction may reveal important insights	What are the trade-offs between plasticity in one behaviour versus another? Does plasticity in one behaviour facilitate consistent, fixed expression of another behaviour? Are there cognitive limits to expressing multiple behavioural plasticities?
Change in patterns of plasticity across environments. Shown is the behaviour of a single population in two environments (open and closed circles)	Different selective pressures may maintain different correlations in different populations	Examining correlational patterns of plastic behavioural phenotypes across different environments. Invasive species may serve as a natural experiment	Do invasive species have weaker correlations in plasticity in their initial native habitat? Do reduced selection pressures in invaded environments allow traits to become unlinked, thus making them effective invaders? How quickly do behavioural correlations deteriorate when this happens? Or do they generally become stronger?

predators (Fischer et al., 2016) and sticklebacks exposed to native predators (Bell & Sih, 2007) both showed increases in among-individual variation and among-individual correlations in behaviour. The simultaneous changes in multiple behaviours were observed in a single generation, indicating evidence of correlated behavioural plasticity. Changes in just one behaviour were insufficient; it was rather the concerted change across multiple behaviours that best allowed individuals to survive predation (Bell & Sih, 2007). The speed with which these changes happened (within a generation) highlight how correlated behavioural plasticity can be an important tool in an organism's toolbox to respond quickly to rapid environmental change.

A final implication of correlated behavioural plasticities that we explore here is that they may explain the lack of strong relationships between states and individual behaviour. States refer to physiological status of an individual, such as hormonal, metabolic or energy reserve state. State-dependent feedbacks are one of the current major hypotheses to explain the continued maintenance of consistent individual differences in behaviour within populations (Sih et al., 2015). However, currently, there is limited support for stable states contributing to consistent individual differences in mean

behaviour (Laskowski, Chang, et al., 2022). A meta-analysis found that only 5% of the among-individual variation in behaviour was explained by variation in state variables (Niemelä & Dingemanse, 2018). Dochtermann (2023) recently extended these state-dependent behaviour models to include more than one behaviour. This work shows that if states influence more than one trait, then even modest feedbacks can generate patterns of correlated plasticity among two different behavioural traits. Importantly, the type of feedback (positive versus negative) can shift the strength and direction of these correlations in predictable ways (Dochtermann, 2023). There is reason to believe that underlying states may be better linked to behavioural plasticity than just mean level differences in behaviour. For example, a study by MacGregor et al. (2021) showed an interaction between hunger state, individual behaviour and behavioural plasticity: when given the opportunity to forage, sticklebacks that exhibited, on average, bolder behaviour also exhibited greater plasticity in their refuge use behaviour whereas shyer sticklebacks exhibited far less plasticity in refuge use.

Metabolic rates in particular have received considerable attention as putative state variables influencing individual behavioural variation (Biro & Stamps, 2010; Careau et al., 2008; Holtmann et al., 2017;

Mathot et al., 2019). Rather than focusing on feedbacks between mean state and behaviour, higher degrees of plasticity in one trait may enable higher degrees of plasticity in another (Table 1, positive correlations). For example, mice with greater aerobic scope, that is, plasticity in their metabolic rates, also exhibited greater plasticity in running behaviour (Biro et al., 2018). Furthermore, there was also greater among-individual variation in the degree of behavioural plasticity among those individuals that also had high aerobic scope. This suggests that low plasticity in metabolic rate (i.e. scope) may constrain the plastic expression of other behaviours, especially those related to energy acquisition (Mathot et al., 2019). If the degree of plasticity in different behavioural traits is correlated, then it may be especially difficult to find correlations in *average behaviours* as highly plastic individuals will show greater variation in behaviour over time. Exploring how the fixed or plastic expression of one behaviour may constrain (or facilitate) plasticity in other behaviours is a promising next step to better understand the feedbacks that may occur between states and behaviours.

UNDER WHAT CONDITIONS WILL CORRELATED BEHAVIOURAL PLASTICITIES BE MOST IMPORTANT?

Correlated behavioural plasticities can have important consequences for several aspects of animal behaviour, ecology and evolution; their impacts are likely to be most apparent when coordination of multiple plastic behaviours is highly adaptive. Here we highlight several of these scenarios by focusing on the role of correlated behavioural plasticity in animal signalling, social contexts and in the face of seasonal and environmental changes.

Animal Signalling

A study by Berg (1960) investigated correlated phenotypes, or 'correlation pleiades', by conducting a taxonomic comparison of herbaceous plants and their flowering traits. Berg predicted that correlated phenotypes are likely to be important in reproductive and social interactions because predictable changes in individual phenotypes are essential for successful communication. Indeed, he found that plant species with specific pollinators (e.g. insects) had more tightly correlated phenotypes, especially in traits associated with attracting pollinators. To attract pollinators, plants need to provide a reliable signal, resulting in phenotypes such as flower size or colour becoming correlated. Berg then suggested that these traits no longer respond individually to fluctuations in the environment, but rather respond to changes in the other traits to produce a tightly integrated and highly reliable signal.

Drawing inspiration from this classic study, we predict that correlated behavioural plasticities are likely to be especially relevant when signalling, either between or within species, is relevant to an individual's fitness. In animal behaviour, signalling and cues can be especially complex. Courtship, for example, often requires the coordinated expression of several traits such as vocalizations, visual displays or pheromones. The absence of just one of these behaviours or an uncoordinated pairing can decrease an individual's fitness. Individuals trying to attract a mate will need to vary the intensity with which they display depending on the physical location, time of year, receptiveness of their potential partner or environmental conditions such as predator presence (Andersson, 2019). For example, male sage grouse (*Centrocercus urophasianus*) can alter both their display rate and quality of calls to attract females. Males that show positive correlations in the magnitude of plasticity in both display rate and call quality were most successful; males that did not exhibit this correlated plasticity were less successful (Patricelli & Krakauer, 2010). And so correlated

behavioural plasticities can improve individual fitness when signals are multimodal and/or involve several coordinated behaviours.

Reciprocal Social Interactions

Correlated behavioural plasticities are likely also important when individuals repeatedly interact with each other and so may need to adjust their behaviour during or between interactions. A classic theoretical example is the Hawk—Dove game, where plastic behaviour, that is, the 'tit-for-tat' strategy, is the evolutionarily stable strategy. The plasticity here comes from the focal individual changing their behaviour based on what their partner previously did. This strategy plays well in models and simulations; there is also evidence for animals across taxa using a tit-for-tat strategy (Dugatkin & Alfieri, 1991; Godard, 1993; Hauser et al., 2003; Schweinfurth & Taborsky, 2020). If individuals are interacting across many social contexts with the same partners, then plastically adjusting several behaviours can help individuals navigate the complex social landscape. Particular strategies (i.e. suites of behaviours) may be more beneficial with one type of partner (e.g. when interacting with a dominant individual) compared to a different partner (e.g. when interacting with a subordinate individual) and so an individual's success may stem from their ability to produce coordinated shifts in multiple behaviours. Correlated plastic behaviours may also be important as social animals engage with partners in different contexts. For example, an individual that would reciprocate a positive grooming interaction might do well to also cooperate when foraging. Evidence for multiple plastic behavioural strategies can be found in chimpanzees, *Pan troglodytes*, which are more likely to exchange food with an individual if they recently had a positive grooming interaction (de Waal, 1997). By examining correlated behavioural plasticities, we may be able to make predictions about how social groups form or stabilize and the strategies that underpin the interaction games that play out within them.

Seasonal and Environmental Changes

Generally, phenotypic plasticity is predicted to persist in variable but predictable environments or extreme environments such as urban environments or environments with dramatic seasonal changes (Bradshaw, 1965; Scheiner, 1993; Tufto, 2000). In particular, the variability and reliability of environmental cues are essential to maintaining plasticity (Snell-Rood & Ehlman, 2021). Additionally, among-generation temporal heterogeneity favours plasticity, but in general, spatial variation favours plasticity more than temporal variation (Scheiner, 2013). This is especially important for animals, which can move between environments quite rapidly, thus requiring extremely plastic traits like behaviour to mediate these dramatic changes. The cost of plasticity, i.e. maintaining the ability to be plastic or the actual cost of plastically adjusting a phenotype, remains difficult to measure (Table 1). However, empirical work suggests that the true cost may not be the maintenance of plasticity, but the cost incurred by occasionally displaying the incorrect phenotype and experiencing low, or even zero, fitness (Leung et al., 2020). In this study, algae (*Dunaliella salina*) were exposed to environmental conditions that differed in predictability, but not variability, of salinity for 500 generations. Algae that experienced more unpredictable salinity levels evolved lower plasticity in cell shape and internal structure because attempting to plastically track the environment led to instances of extreme mismatches and hence zero fitness. If environments vary across multiple axes, for example temperature, resource availability or social landscapes, then correlated behavioural plasticities can help individuals more easily navigate such multifaceted changes.

In addition to favouring plasticity, spatiotemporal variation in the environment is also predicted to contribute to the maintenance of consistent individual differences in mean behaviour (Dingemanse et al., 2004; Sih et al., 2004). Environments where multiple cues vary predictably may be a promising place to begin looking for correlated behavioural plasticities. For example, birds that migrate undergo extreme changes in environmental conditions and similarly dramatic changes in physiology and behaviour. The golden-crowned sparrow, *Zonotrichia atricapilla*, maintains consistent personality across years and also forms semi-stable social groups composed of both males and females where they overwinter (Block et al., 2021; Shizuka et al., 2014). When they migrate to their breeding grounds in Alaska and Canada, males become territorial and begin singing, two behaviours which are largely absent in their overwintering habitats. Studying correlated behavioural plasticities was not the explicit goal of this study, but the long-term behavioural data available from systems like this could be an excellent resource. In general, migratory species that occupy distinct habitats during predictable times of year may be an excellent system to begin exploring the adaptive value of correlated behavioural plasticities because they may have stronger correlations, thus impacting how they respond to selective pressures. Furthermore, understanding which behaviours are plastically responding to these environmental shifts and whether they are correlated may reveal interesting patterns driving migration, mating, or even sociality. Patterns of correlation may reveal essential linkages that act as precursors to sociality.

A key prediction of classic plasticity research is that developmental, or irreversible, plasticity will be favoured when the environment of the parent does not match that of the offspring, also known as coarse-grained variation (Levins, 1963; Snell-Rood, 2013). Alternatively, reversible plasticity is favoured by environmental changes within the lifetime of an individual; this is known as fine-grained variation. Often, the coarse-grained variation that selects for developmental plasticity is a result of seasonality or dispersal strategies. For example, marine invertebrates with low dispersal exhibit lower levels of plasticity when compared with species with higher dispersal rates (Hollander, 2008). However, because behaviour is often reversibly plastic, and because most of the variation is found within (as opposed to between) individuals (i.e. among-individual differences in behaviour only explain about 0.37 of behavioural variation; Bell et al., 2009), a focus on fine-grained environments might be a more fruitful place to begin examining correlated behavioural plasticities. Understanding the mechanisms that govern the synchronicity of different plastic behaviours can reveal how this variation is maintained. How might these two types of environmental grains lead to possible conflict or correlation between developmental and reversible plasticity?

Here we now provide a hypothetical example of how to study correlated behavioural plasticity. Consider guppies, *Poecilia reticulata*, a species of fish that engages in cooperative predator inspection, as well as fighting with each other to gain access to mates. The expression of both of these behaviours can change as a result of familiarity with the conspecifics they are cooperating or fighting with; they are expected to fight less and inspect more with familiar individuals (Dugatkin & Alfieri, 1991; Price & Rodd, 2006). Thus, the plastic expression of both behaviours depends on the ability of individuals to discriminate between familiar and unfamiliar conspecifics. By examining possible correlations between these two behaviours, we might be able to generate hypotheses about how these two behaviours are mechanistically linked. On the one hand, the sensory mechanisms to recognize familiar individuals are certainly shared whether the recognition is happening in a mating or an antipredator context. On the other hand, the downstream physiological and cognitive mechanisms, as well as the selective

consequences of how to behave once this recognition occurs may be very different. To estimate the presence and extent of correlated plasticity in these traits, both inspection behaviour and fighting behaviour could be measured when a focal individual is presented with a range of conspecifics with increasing familiarity. The behavioural responses across this familiarity gradient could then be used to examine among-individual (i.e. within a single population) correlations in plasticity using the methods outlined in O'Dea et al. (2021). Briefly, repeated measures data collected in both behaviours across an environmental gradient, here, familiarity, can be modelled using bivariate models where the random variance−covariance structure can directly estimate the covariation in plasticity in each trait (i.e. equations 10−15 in O'Dea et al., 2021; Fig. 1). Such comprehensive data collection used to be prohibitive for many studies, but advances in affordable computing and ready-to-use automated tracking has dramatically increased both the quantity and nuance of behavioural data collection (Jolles, 2020, 2021; Jürgen Mönck et al., 2018; Mathis et al., 2018; Walter & Couzin, 2021).

The magnitude of plastic responses to familiarity can help us determine whether these behaviours are mechanistically linked or not and what costs might be incurred by co-expression. For example, a positive correlation between the magnitude of plasticity in each trait suggests that there may be an underlying mechanism that controls the degree of plasticity in both (Fig. 2f; Table 1); future work could then more closely investigate the precise mechanism. For example, this might be expected if the sensory machinery of an individual is key to that animal detecting and recognizing both potential competing males and potential cooperators. Blinding individuals to particular sensory cues in both contexts, say, by preventing the transmission of chemical cues in the water or only allowing chemical cues (but not visual cues), and then measuring the animals' behaviour again could begin to tease apart whether sensory constraints are major drivers of correlated plasticity. Alternatively, a negative correlation between plasticity magnitudes would be more suggestive of trade-offs between the two behaviours (O'Dea et al., 2021; see Fig. 2c; Table 1). However, if there is no correlation, then this suggests that the two traits are not mechanistically linked (O'Dea et al., 2021). Similar comparisons of magnitude between individuals might allow us to better understand the possible costs and benefits of plasticity. For example, if a positive correlation in both cooperative and aggressive behaviours is dependent on a fish having good body condition, then this might suggest that only individuals with sufficient resources can meet the energetic needs necessary to support the cognitive ability of discriminating between familiar and unfamiliar individuals. A further extension of this work could explore how patterns of correlated plasticity change across different populations. For example, based on predation pressure, it may be less beneficial for individuals to adjust the intensity of mate competition if mating displays are especially prone to attracting predator attention. This could erode plasticity correlations in populations with high predation, for example, compared to populations with lower predation.

SUMMARY AND FUTURE DIRECTIONS

Accurately quantifying plasticity in behaviour will require more than just a few repeated measurements on each individual as the statistical techniques to estimate reaction norm slopes, and correlations among them, can be quite data hungry (Dingemanse & Dochtermann, 2013; Mitchell et al., 2021; O'Dea et al., 2021). However, we believe that the field of animal behaviour is at the beginning of an era where such sample sizes are well within reach, although some experimental systems may be more amenable to
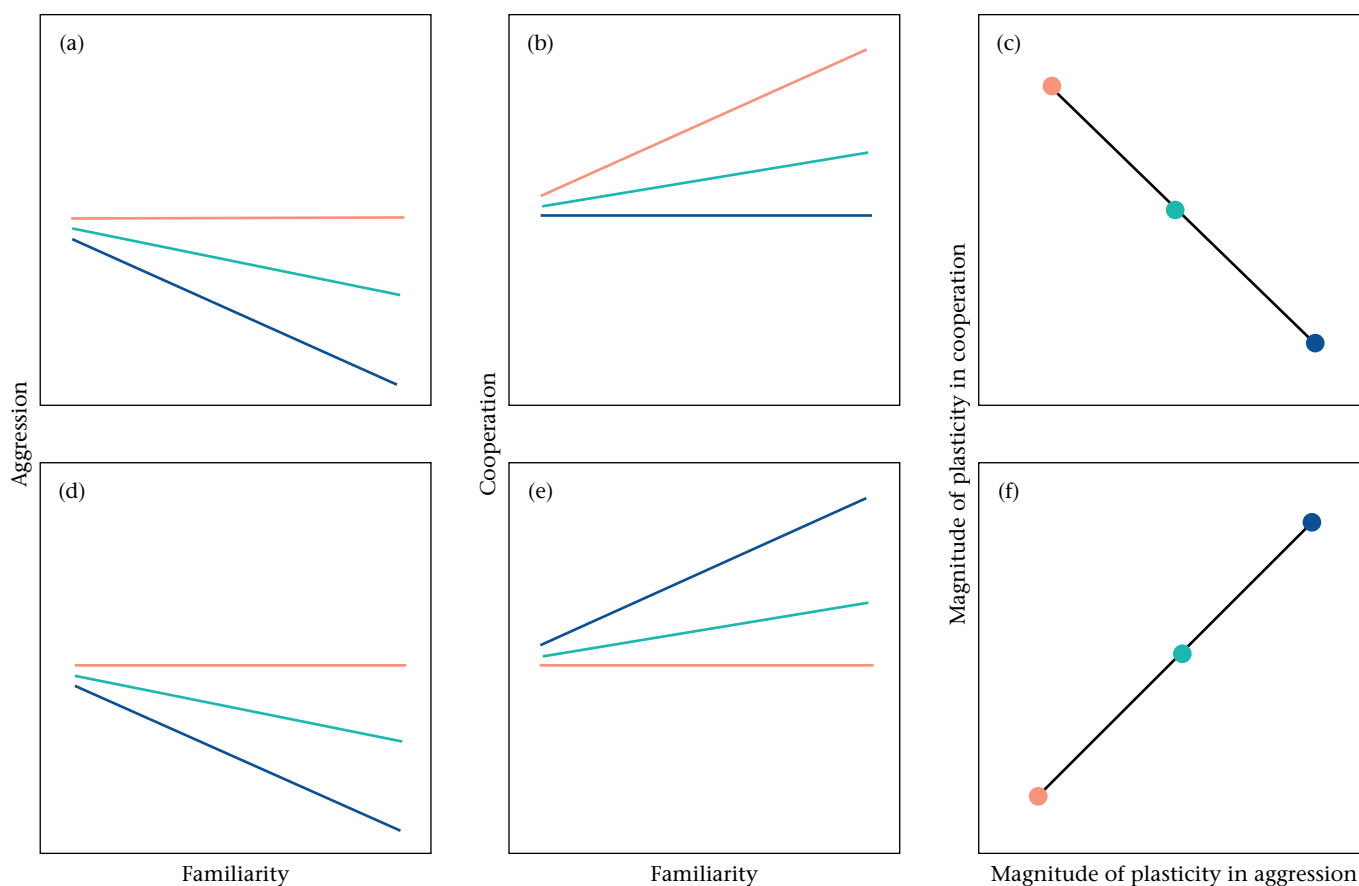
Figure 2. Intensity of fighting for mates and cooperation in predator inspection are measured among three individuals (pink, green and blue lines) across a gradient of increasing conspecific familiarity. In (a–c), there is a negative correlation between the magnitude of behavioural plasticity (c); individuals that are more responsive to familiarity with competitors are less responsive to familiarity during predator inspection. In (d–f), there is a positive correlation in behavioural plasticities (f) such that individuals that more strongly adjust their mating aggression also adjust their predator inspection when faced with more familiar conspecifics.

collecting the necessary high-resolution data. Nevertheless, such high-resolution data need not be confined to the laboratory. Some researchers have designed clever apparatuses that allow animals to express particular behaviours repeatedly in the wild such as foraging tasks in blue tit, *Cyanistes caeruleus* (Aplin et al., 2013) and chickadee populations (Sonnenberg et al., 2019). Advances in remote tracking through global positioning system (GPS) tags or passive integrated transponder (PIT) arrays offer a useful method to collect many data points on movement and location-related behaviours, even on wild animals. For example, Hertel et al. (2021) used GPS collars to track daily movement patterns in a population of brown bears, *Ursus arctos*. These rich data allowed researchers to quantify individual variation in behavioural averages, slopes and predictability. Strandburg-Peshkin et al. (2015) used similar collars on baboons. These data were collected on individuals in the same troop, allowing the researchers to investigate how individuals changed their behaviour in response to each other, a form of socially induced behavioural plasticity. For laboratory-based animals, sophisticated automated-tracking systems are becoming more common, allowing researchers to collect extremely high-resolution data on individuals in known environments (de Bivort et al., 2022; Jolles, 2020; Walter & Couzin, 2021). For example, Laskowski, Bierbach, et al. (2022) tracked individual behaviour of clonal fish from birth through the first 10 weeks of their lives, allowing them to follow how several individual behavioural traits changed across ontogeny. While laboratory-based studies may lack some of the ecological realism of field-based work, these types of

studies allow researchers to mimic changes in environmental gradients that may be especially relevant for different axes of behavioural plasticity such as aspects of seasonal change or the social environment.

In summary, we find that the steps outlined by Berg (1960) for investigating 'correlation pleiades' may serve as a useful guide for future work on correlated plastic behaviours. Berg emphasized that describing the *benefits* of phenotypic correlations is essential to conducting targeted research. Necessarily, this requires describing the variation in correlation among taxa or populations. This can best be accomplished by finding instances where behavioural plasticities are correlated and where they remain unlinked; research on behavioural syndromes has already provided a first step. The next steps will be to expand beyond correlations in average behaviour to examine correlations in plasticity.

Author Contributions

K. Sheehy provided conceptualization and wrote the original draft. K. Laskowski filled a major advising and writing role, providing major edits and revisions.

Declarations of Interest

None.

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