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Insights into adaptive behavioural plasticity from the guppy model system

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Behavioural plasticity allows organisms to respond to environmental challenges on short time scales. But what are the ecological and evolutionary processes that underlie behavioural plasticity? The answer to this question is complex and requires experimental dissection of the physiological, neural and molecular mechanisms contributing to behavioural plasticity as well as an understanding of the ecological and evolutionary contexts under which behavioural plasticity is adaptive. Here, we discuss key insights that research with Trinidadian guppies has provided on the underpinnings of adaptive behavioural plasticity. First, we present evidence that guppies exhibit contextual, developmental and transgenerational behavioural plasticity. Next, we review work on behavioural plasticity in guppies spanning three ecological contexts (predation, parasitism and turbidity) and three underlying mechanisms (endocrinological, neurobiological and genetic). Finally, we provide three outstanding questions that could leverage guppies further as a study system and give suggestions for how this research could be done. Research on behavioural plasticity in guppies has provided, and will continue to provide, a valuable opportunity to improve understanding of the ecological and evolutionary causes and consequences of behavioural plasticity.

1. Introduction

Behaviour is often distinguished from other phenotypic dimensions by being highly plastic on relatively short, within-lifetime, time scales (but see [1]). Therefore, adaptive behavioural plasticity may be especially important for success in variable environments, given that behavioural traits can be highly environmentally sensitive. However, the evolution and expression of behavioural plasticity involves complex interactions spanning spatial and temporal scales, variable environments and genetic, neurobiological, and endocrinological traits. Moreover, behavioural plasticity itself is multi-faceted. This complexity presents a significant challenge for untangling the underlying ecological and evolutionary processes involved in the expression and maintenance of behavioural plasticity. Accordingly, gaps remain in our understanding of the ecological contexts that favour the evolution of behavioural plasticity and what proximate mechanisms underlie its expression [2]. Filling in these gaps is no simple task, but this research can be facilitated by using organisms that are easy to manipulate in the laboratory and in the field, have rapid generation times, traits that can be easily measured, and for which we possess a wealth of existing knowledge on their behavioural and evolutionary ecology. One organism that represents a powerful system for addressing the aforementioned knowledge gaps is the Trinidadian guppy (*Poecilia reticulata*), henceforth guppy.

Guppies are small, tropical, freshwater fish native to Trinidad and Tobago as well as other countries in northern South America with a rich history of

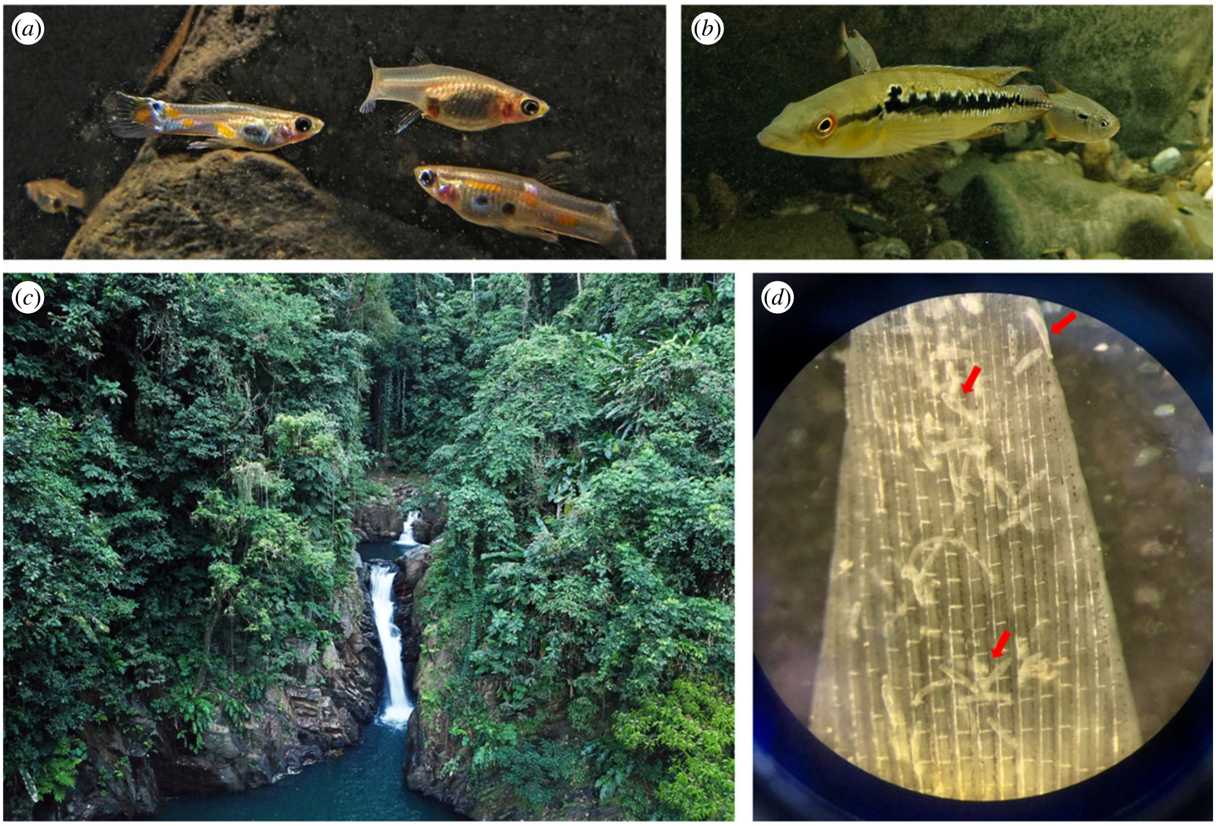

Figure 1. Ecology of Trinidadian guppies. In Trinidad, guppies live in streams separated by waterfalls (*c*) that act as natural barriers to many predators, separating habitats above and below waterfalls into areas of low and high predation risk [6]. (*a*) Male and female guppies; note the sexual dimorphism in size and coloration. (*b*) A common guppy predator, *Crenicichla frenata*. (*d*) A common guppy parasite, *Gyrodactylus* spp.—red arrows point to a few particularly clear examples. Photograph credits: waterfall—Andrew Hendry; guppies, *Crenicichla*—Paul Bentzen; *Gyrodactylus* spp.—Katrina Di Bacco.

research leading to many insights for evolutionary ecology (for overviews, see [3–6]). This includes work over the last few decades, reviewed below, that has shown that guppy behavioural plasticity can be considerable, vary across environments, and have important ecological and evolutionary consequences. In nature, guppies are often studied in Trinidad where the streams they inhabit can differ in ecological factors such as predation risk, primary productivity, population density and parasite prevalence—providing a natural laboratory with different ‘experimental treatments’ for studying plasticity (figure 1) [3–6]. Furthermore, guppies are a highly invasive species and have been domesticated, providing unique opportunities for studies of plasticity in novel habitats that are not available in other behaviour model systems such as stickleback, which have not been domesticated, and zebrafish, which have not been as widely invasive [7]. Guppies also possess neurobiological traits that make them particularly interesting for the study of behavioural plasticity. Teleost fish such as guppies demonstrate extensive adult neurogenesis, the production of new neurons, at a rate drastically higher than that of mammals [8]. Environmental factors can induce rapid plastic changes in neuroanatomy, giving researchers the opportunity to study how neuroanatomical and behavioural plasticity interact. Genetic and neurobiological resources for guppies, including a neuroanatomical brain atlas [9] and annotated genome [10] provide new opportunities to use guppies to explore the underlying mechanisms of behavioural plasticity in greater detail. Insights into behavioural plasticity found in guppies can provide information about how behavioural plasticity evolves and be informative for other vertebrate systems.

In this review, we provide a non-exhaustive overview of some key insights that guppy research has contributed to our understanding of behavioural plasticity and propose ways in which guppies can be used to answer open questions in the field. We first outline the different categories of behavioural plasticity with examples where guppies have been shown to express each type. Second, we discuss three ecological contexts in which behavioural plasticity has been studied in guppies and the main takeaways from each context. Third, we provide information on current and possible future research within three types of underlying mechanisms of behavioural plasticity. Finally, we identify three major outstanding questions and propose ways in which guppies could be used to tackle these questions.

2. Types of behavioural plasticity

Three broad categories of behavioural plasticity can be identified [11]: (i) contextual behavioural plasticity, expressed in response to variation in the immediate environment; (ii) developmental plasticity, expressed in response to environmental variation experienced earlier in the organism’s lifetime; and (iii) transgenerational plasticity, expressed in response to environmental variation experienced by previous generations (figure 2). Being specific about the type of behavioural plasticity allows for better cross-study comparisons and allows investigations into the relationships between different types of behavioural plasticity [11,12]. Guppies have been shown to express behavioural plasticity across all three categories, making them an ideal study system to explore these relationships.

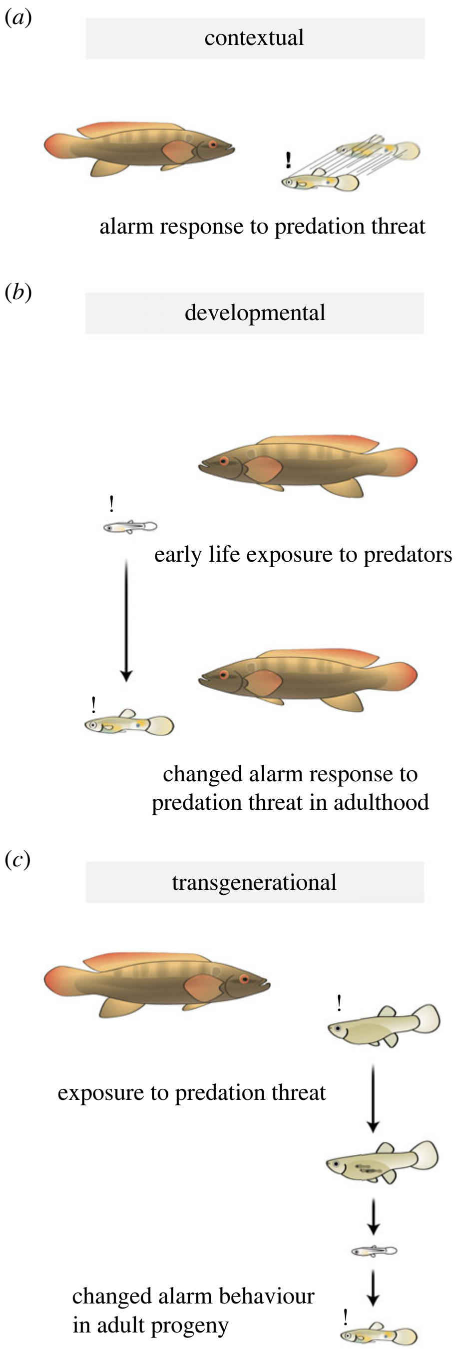

Figure 2. Overview of types of behavioural plasticity. (*a*) Contextual plasticity describes behavioural responses to stimuli in the immediate environment, such as the anti-predator behaviour 'dashing' in the presence of a predator. (*b*) Developmental plasticity describes behavioural plasticity related to previously experienced environmental variation and includes early life exposure to predation threat. (*c*) Transgenerational plasticity describes behavioural plasticity that is influenced by environmental variation acting on previous generations such as maternal exposure to predation threats.

(a) Contextual plasticity

Contextual behavioural plasticity is also called activational plasticity, behavioural flexibility or responsiveness or 'innate' behavioural plasticity [2]. Guppies exhibit contextual behavioural plasticity across many ecological conditions. In response to predation threat, guppies increase anti-predator behaviours including increased shoaling, dashing, freezing, predator inspections and area avoidance [13], and also shift foraging rates [14,15]. Male guppies alter their mating tactics in response to changes in the social environment [16], light environment [17] and parasite infections [18], while female guppies exhibit shifts in mate choice when exposed to predators [19]. These studies demonstrate that guppies respond to many different environmental cues to adjust behaviour to current conditions through contextual behavioural plasticity.

(b) Developmental plasticity

Compared with contextual plasticity, developmental plasticity has a slower phenotypic response time, which trades off with longer-lasting phenotypic integration [11]. Multiple types of behavioural plasticity can be considered a form of developmental plasticity, including temporal plasticity, where a phenotype changes as a function of age or time, and classical developmental plasticity, in which early life experiences shape behaviour later in life. Individual and social learning are considered a type of developmental plasticity. Ontological shifts in behaviour remain understudied in guppies (but see, [20]), whereas learning and classical developmental plasticity have been studied more extensively.

Given their relatively short generation time (110–210 days [21]), guppies have provided an excellent system for investigating the relationship between early life environmental experiences and adult behaviour [22–24]. For example, adult guppies can cannibalize young fry, exposing them to predation early in life and potentially priming individuals to face this strong selective pressure later in life [6]. Accordingly, juveniles raised in the presence of adult guppies develop into adults with increased shoaling and alarm responses and smaller body size combined with deeper caudal peduncles—behavioural and morphological traits that are also observed in guppies living in environments with major predators [25]. Guppies respond to a variety of early life cues, although the adaptive potential of the response is not always clear; for instance, guppies that experience an unpredictable food supply [26] or predation risk during early life [22] become bolder and more exploratory than those that experience control environments. While these studies show that developmental plasticity is prevalent in guppies, more work is needed to determine whether this plasticity is adaptive by assessing the fitness consequences of these behavioural shifts.

Guppies are also a valuable system for studying learning, because they learn both individually [27–29] and socially [30,31]. Individually, guppies can solve and learn mazes [28], learn preferences for familiar individuals [32] and learn to numerically discriminate [27]. Socially, guppies readily learn from others about foraging sites and predation threats [30,31,33]. When exploring a novel environment, plasticity in shoaling behaviour may allow guppies to group with heterospecifics, potentially providing anti-predator and foraging benefits [34]. These studies show learning may have adaptive benefits; however, learning itself may also be a plastic trait that can be shaped through developmental plasticity (i.e. individuals develop into adults that are more or less likely to learn). For example, a developmental manipulation found that guppies exposed during early life to adults that provided useful foraging information exhibited social learning, unlike those exposed to other or no adults [23]. The extent to which learning is a plastic trait itself remains unclear but these studies do show that learning and other forms of developmental plasticity can interact to change behavioural outcomes.

(c) Transgenerational plasticity

Transgenerational plasticity when defined broadly includes both parental effects and impacts on later generations (e.g. grand offspring) [35]. It may occur through non-genetic inheritance such as the transfer of gene products, nutrients or epigenetics, or it can occur when previous generations alter the environment an individual experiences, such as through differences in habitat selection or parental care and investment [35]. This type of behavioural plasticity is understudied, although recent studies report the existence of transgenerational behavioural plasticity in guppies [36,37].

Parental effects, especially maternal effects, have been the focus of much of the work on transgenerational plasticity in guppies. While guppy mothers provide no post-natal parental care, guppies are live-bearing and mothers probably pass information to offspring *in utero* [38,39]. Guppy mothers exposed to predation cues during gestation produced offspring with increased exploratory behaviour [36]. The adaptive impacts of this behavioural shift are unknown; however, increased exploratory behaviour may increase offspring propensity to disperse, potentially allowing individuals to leave high-predation areas. While maternal effects have strong impacts on juvenile behaviour, these impacts can lessen significantly with age [40], demonstrating that transgenerational effects may vary in their importance over lifespan. Transgenerational behavioural plasticity has also been shown paternally in guppies. Guppy behavioural plasticity induced by paternal exposure to methylphenidate hydrochloride (Ritalin) impacted the behaviour of offspring and great-grand offspring in open field tests [37], suggesting that non-genetic factors present in sperm can have transgenerational impacts on behaviour across several generations. Together, this research demonstrates the existence of transgenerational behavioural plasticity via both maternal and paternal routes, and shows that the importance of transgenerational effects can vary over individual lifetimes.

3. The ecological context of behavioural plasticity

Comparing populations that differ in their selective environments provides a route to investigate which ecological factors impact the evolution of behavioural plasticity. Guppies can easily be sampled from a wide array of ecological contexts and, as such, have already been used to investigate a number of questions regarding the ecological drivers of behavioural plasticity. Here we review insights gleaned from three well-studied ecological contexts in guppies: predation, parasitism and turbidity (figure 3).

(a) Predation

Predation is one of the strongest selective pressures for many wild guppies [47], representing an immense threat to lifetime fitness [48] and exerting considerable pressure on behavioural trade-offs [49]. Predation pressure varies across populations and within lifetimes as individuals move between habitats or experience varying levels of predation stress over time and space [50]. Recent predation events can be detected by the presence of alarm cues, substances released upon mechanical damage to the skin of many fish species that induce immediate plastic anti-predator behaviours [13,51]. Owing to this reliable cue and environmental variability in predation risk, guppy predation responses lend themselves well to the study of behavioural plasticity and, accordingly, have been used to test several related hypotheses.

The degree of plasticity an animal should exhibit in response to predation threat can be predicted by the risk allocation hypothesis, which posits that prey cannot continually respond to predation threats under consistently high predation risk [52]. These situations lead to the seemingly paradoxical phenomenon where responses to predation decrease as predation pressure increases. Guppies from sites with many major guppy predators (high predation) continue feeding when a predator stimulus is present,

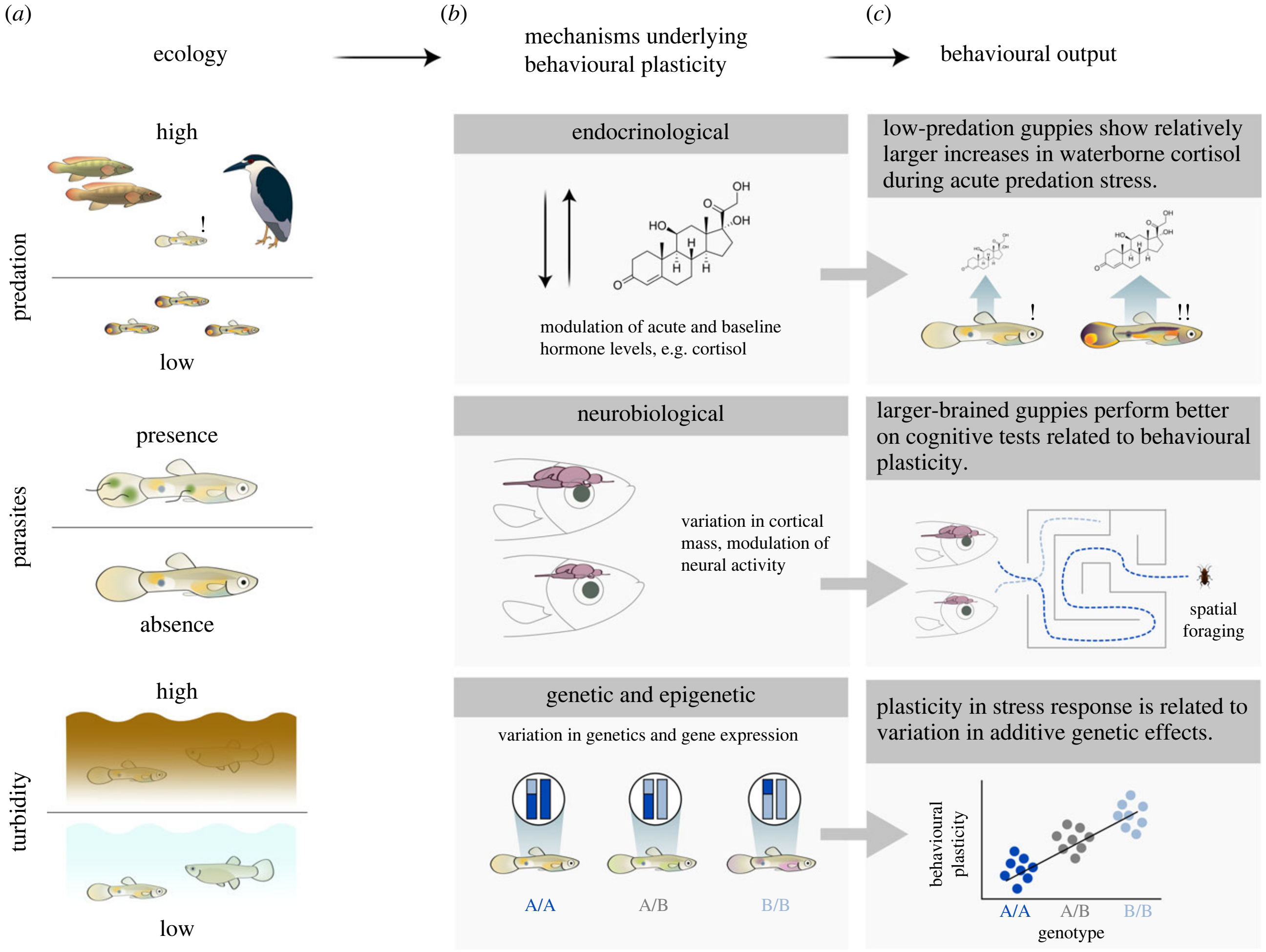

Figure 3. Overview of example ecological contexts and mechanisms of behavioural plasticity. (*a*) Guppies face differing levels of predation risk, parasitic infection and water turbidity. (*b*) and (*c*) These contrasting ecological contexts shape adaptive responses directly through within-organism mechanisms, or indirectly through genetic variants. In guppies, modulation of behavioural plasticity has been studied through endocrinological, neurobiological and genetic mechanisms. Endocrinological mechanisms include changes in cortisol levels, which have complex interactions with population and sex [41,42]. Variation in brain size and modulation of neural activity has been linked to various measures of behavioural plasticity [43,44]. Behavioural plasticity is influenced by additive genetic variation [45] and rapid shifts in gene expression [46].

whereas guppies from sites with few or no guppy predators (low predation) react in a sensitive manner by completely halting foraging [15]. By maintaining a lower baseline reaction to predation stress, high-predation guppies can continue important activities in high-risk environments and react more appropriately when predation risk increases.

Individuals experiencing chronically high predation risk may also exhibit graded risk-sensitive behavioural plasticity, allowing them to adjust their responses according to the risk level. Guppies from environments with multiple predatory fish species grade their anti-predator response when presented with a predator species based on the degree of threat it poses, with less dangerous species eliciting weaker responses [53]. Moreover, when exposed to conspecific alarm cues across a range of concentrations that mimic variable predation risk, guppies from high-predation environments exhibit a graded response to predation cues depending on the concentration of the alarm cue, while guppies from low-predation environments exhibit a non-graded hypersensitive response regardless of alarm cue concentration [51,54]. Adjusting predation response according to risk level enables guppies to optimize the trade-off between anti-predator responses and other activities.

The cost of not responding optimally upon an initial encounter with a novel predation threat can be high. Guppies can help us understand how animals can mitigate this cost through phenotypically plastic neophobia, the avoidance of novel stimuli, a phenomenon induced through exposure to elevated background predation risk in both the laboratory and field [55]. Induced neophobia may reduce the short-term costs of an initial encounter with novel predators, giving an individual time to express anti-predator developmental behavioural plasticity through learning. Whether phenotypically plastic neophobia acts as a general response to increased levels of background risk in the environment across animals remains unknown.

Research on behavioural plasticity in guppies has thus far shown that predation environment can impact not only the level of behavioural plasticity favoured, through support of the risk allocation hypothesis, but also the nature of the plasticity expressed, such as through risk-sensitive grading and plastic expression of neophobia. However, many studies dichotomize populations into high- versus low-predation sites while, in reality, populations experience a gradient of predation due to the varying predator species across sites and time periods [56]. It would be of interest to investigate whether populations adapt to continuous environmental gradients through fine-scale local adaptation or instead predominantly use plasticity. With varying predator species the 'form' of predation also varies as these species engage in different predatory tactics (e.g. aquatic ambush or stalking) [57].

Guppy populations with diverse predators are exposed to more variable predatory tactics which probably has an impact on behavioural plasticity. Investigating this variability in predation type would allow for a better understanding of the impact of environmental heterogeneity on behavioural plasticity.

(b) Parasites

While predators represent acute, immediate threats to well-being, parasites can reduce overall fitness during infection and can be deadly for their hosts over a longer period. The most well-studied parasites of guppies are *Gyrodactylus turnbulli* and *Gyrodactylus bullatarudis* [58]. *Gyrodactylus* spp. are small, viviparous ectoparasites that can spread by jumping from one host to another during close contact [59] and feed on host mucus and epithelial tissue. Infections can be fatal for guppies due to excessive skin damage or secondary bacterial infections [60]. Natural guppy populations experience temporal and spatial variation in parasitism and guppies respond to both visual and chemical cues of *Gyrodactylus* infection that may induce behavioural plasticity. Our understanding of how guppies manage parasitism risk reveals how animals may behaviourally avoid and/or mitigate the costs of infection burden.

Adaptive behavioural plasticity may allow guppies to avoid infection or to counteract negative fitness effects incurred during infection. Since *Gyrodactylus* spread through contact between guppies, behavioural plasticity in shoaling and social network dynamics may act as a form of behavioural immunity. Guppies in a semi-natural setting avoided shoaling with an introduced infected individual by increasing shoal fission events [61]. Behavioural plasticity can also reduce the impacts of *Gyrodactylus* infections. For example, infected guppies may facilitate transmission by increasing contact with uninfected conspecifics, potentially alleviating individual infection burdens [62]. Additionally, infected guppies prefer warmer waters at the upper thermal tolerance of their parasite, potentially using these warmer waters to self-medicate (i.e. 'behavioural fever') [63]. Guppies also increase foraging to compensate for increased energetic demands during infection [64]—although this behavioural change may increase predation risk and reduce time available for courtship [18].

Gyrodactylus infection can reduce reproductive success as uninfected conspecifics avoid infected individuals [65]. Uninfected males display less to infected than uninfected females [66], and uninfected females prefer uninfected males [67]. However, infected female guppies may compensate for parasitism with changed mating behaviour, showing no preference for attractive over unattractive males [66]. Behavioural plasticity may also maintain fitness enhancing behaviours in specific social contexts: in the absence of females, infected male guppies with higher tolerance (defined by per-parasite change in activity level) have higher activity levels than males with lower tolerance, but in the presence of females, males with lower tolerance maintain activity levels at the same level as males with higher tolerance [68]. This plasticity allows males to conceal the negative impacts of their infection, thereby probably maintaining a higher reproductive success.

Studies on parasite-induced behavioural plasticity in guppies provide evidence that behavioural plasticity may be an adaptive response to avoid infection or deal with current infection. However, work investigating how behavioural plasticity influences transmission and infection dynamics, and the resulting impacts on individual survival and reproductive success, is needed to analyse the extent to which this plasticity is adaptive. Since predation and parasitism often overlap in guppy populations, the opportunity also exists to investigate how conflicting fitness trade-offs influence behavioural plasticity.

(c) Turbidity

Water turbidity, the level of light scattered in a liquid, has been steadily increasing in freshwater habitats worldwide due to anthropogenic impacts. Decreases in light availability reduce the visual cues and communication available and impact a variety of behaviours in fish such as shoaling [69], anti-predator responses [70], foraging [71] and mating behaviour [72]. Guppies are exposed to natural fluctuations in turbidity daily, weekly and seasonally, but as Trinidad is increasingly impacted by rock quarries and deforestation, guppies are being exposed to longer and more intense bursts and higher baseline levels of turbidity in some streams [73,74]. Increased water turbidity may interact with behavioural plasticity by interrupting cues needed to induce certain plastic responses. However, guppies may also exhibit behavioural plasticity in response to turbidity to ameliorate its impacts on fitness-associated behaviours.

Increased turbidity can limit a guppy's ability to visually detect predators or conspecifics. Guppies tested in turbid waters are less active and form smaller shoals compared with guppies tested in clear waters [73,75]. This could be an adaptive response to reduce encounter rate with predators, or it could be due to sensory constraints as individuals are unable to detect conspecifics. Physiological changes can accompany behavioural plasticity. Guppies reared in turbid waters shifted the physiology of the visual system from predominantly mid-wave-sensitive opsins to predominantly long-wave-sensitive opsins which are more important in motion detection [76]. This was accompanied by developmental shifts in behaviour, with an interactive impact of rearing and testing conditions such that when guppies were tested in turbid water, those reared in turbid water increased activity and those reared in clear water decreased activity. These findings show that different types of plasticity may differ in adaptive value, with behavioural changes that occur in conjunction with physiological adaptations being more likely to be adaptive.

Guppy mating is heavily reliant on visual cues with brightly coloured males typically being more attractive to females [77]. Males can perform sigmoidal displays, a form of conspicuous mating that shows off their bright coloration, or can attempt sneak copulations [5]. Turbidity induces shifts in mating behaviour that may be adaptive in an environment with decreased visual cues. Guppies from both turbid and clear streams increased the rate of all mating behaviours when tested in turbid water, potentially to compensate for changes in the visual environment [78]. Guppies from turbid streams also exhibited increased variation in mating behavioural plasticity whereas guppies from clear streams showed high individual consistency in mating behaviour. This high variation in mating behaviour may allow for male guppies from turbid streams to switch between sigmoidal displays, which rely on visual cues, and sneak mating, which is probably beneficial in reduced visibility, depending on current turbidity. Turbidity may also induce developmental behavioural plasticity in mating behaviour and coloration; males reared in turbid water perform fewer sigmoidal displays and have more conspicuous coloration compared with males reared in clear water [79].

While the studies described here show that turbidity can have an impact on guppy behavioural plasticity and that this plasticity can be adaptive, more work is needed to determine whether behavioural plasticity is adaptive in more complex environments. Water temperature has been found to have an interacting effect with turbidity such that guppies were in closer proximity to their predators in warm, turbid waters [80]. There are also likely interacting effects of predation and turbidity due to the reliance of many predators on visual cues, including *Crenicichla*, one of the major guppy predators [74], and the use of visual cues to avoid predators. Studying how these multiple ecological contexts interact will provide a better understanding of behavioural plasticity in more complex environments.

4. Mechanisms of behavioural plasticity

Understanding the mechanisms underlying behavioural plasticity can provide important information about the evolution of behavioural plasticity and its ecological consequences. However, detailed mechanistic investigation can be difficult in large-bodied, long-lived organisms or in organisms without established genetic or neurobiological resources. Guppies provide a tractable vertebrate system with several supportive resources. Here, we discuss insights into the endocrinological, neurobiological and genetic mechanisms underlying behavioural plasticity that have been revealed by guppies (figure 3).

(a) Endocrinological mechanisms

It has been shown in guppies that endocrinology can control the range of behavioural plasticity available to an individual through hormonal reaction norms. In teleosts, such as guppies, the stress hormone cortisol plays a critical role in mounting a behavioural stress response [81]. Acute stress exposure results in transient increases in plasma cortisol levels, which then recover to normal resting levels after removal of the stressor. When exposed to the same stressor multiple times, the levels of cortisol released in response may diminish as individuals become habituated to the stressor. Guppies exposed to the same mild stressor multiple times had lower waterborne cortisol levels in later exposures than earlier ones [82]. Repeated exposure to stressors may shift baseline plasma cortisol levels, leading to changes in the range of hormonal reactive scope available to an individual and therefore the level of behavioural plasticity that can be expressed in response to stressors [83]. High-predation guppies have lower waterborne cortisol levels than low-predation guppies, and guppies reared in the presence of predator chemical cues had lower waterborne cortisol levels than those reared without cues, showing that both evolutionary history and developmental exposure to predation impact cortisol release [41]. This suggests that while acute exposure to predation is likely to result in increased cortisol levels, guppies experiencing prolonged exposure may maintain a lower baseline cortisol level to increase the hormonal reactive scope and range of behavioural plasticity available to them. These results offer further evidence supporting the risk allocation hypothesis, where guppies experiencing chronically high levels of predation stress show decreased reactions to predation.

Sex can influence hormonal stress responses. When experiencing multiple recurring stressors (predation and high rearing density), male guppies release more cortisol than females, and only females reduce cortisol levels over time [42]. This suggests that males have a higher baseline level of cortisol and lower reactive scope compared with females. These sex differences could be due to differing life-history strategies, with males displaying a ‘fast’ life-history involving more risk-taking behaviours, quicker maturation and shorter lifespans. By maintaining a higher reactive scope, females can more rapidly respond to stressors and increase fitness for their comparatively ‘slow’ life-history strategy. Indeed, males will continue to attempt mating during stressful predation threats whereas females are much more plastic, readily engaging in anti-predator behaviours [84].

Thus far, research on endocrinological mechanisms of behavioural plasticity in guppies has provided compelling evidence for interactions between endocrinology and behavioural plasticity, support for the risk allocation hypothesis, and shown an influence of sex on hormonal stress responses. However, current studies remain somewhat limited in scope. Research investigating individual-level differences in cortisol levels have rarely connected these findings to differences in behavioural plasticity, and more work is needed to investigate the role of other hormones and their receptors in influencing reaction norms. It is likely that whole networks of hormones are involved, not just cortisol. Isotocin and vasotocin have been shown to play a role in guppy grouping using intracerebroventricular administration techniques that could be used to study the impact of other hormones on behavioural plasticity [85]. Intracranial administration can also be used to manipulate gene expression using viral-mediated transgenesis [86]. Additionally, guppies have greatly expanded their native and non-native range, even into heavily polluted environments [87], creating new challenges that require integrated endocrinological and behavioural adaptations and providing unique opportunities for research.

(b) Neurobiological mechanisms

Behavioural plasticity is probably functionally linked to specific changes in the form and function of the brain and sensory or perceptual systems. One general hypothesis regarding the neurobiological basis of behavioural plasticity is that greater plasticity is associated with enlargement of the entire brain or of specific brain regions [88–90]. While this hypothesis has typically been addressed with comparative studies (e.g. [90]), the guppy model has been leveraged to facilitate an experimental approach, artificially selecting lines of guppies for both total brain size and the size of a forebrain region, the telencephalon [88,90]. This has revealed impacts on several indices argued to indicate behavioural plasticity, such as habituation to a novel environment [88] and numerical [91], reversal [92] and spatial learning [43], with some results specific to one sex. However, an important issue is that different tests of behavioural plasticity can measure distinct traits [12]. Since neural tissue is metabolically expensive, increases in brain size are expected to balance costs with the benefits of increased functionality [93]. Accordingly, large-brained guppies have smaller guts [91]. However, this is not the case in guppies selected for larger telencephalons, suggesting that evolutionary changes in specific brain regions (mosaic evolution) can provide an energy-efficient route to enhanced behavioural plasticity [90].

Tying real-life environmental conditions to shifts in brain size could increase ecological relevance and potentially reveal which environmental factors favour plasticity. Studies have found that male but not female guppies from high-predation populations have larger brains than those from low-predation sites, and male guppies exposed to predator cues early in life develop larger brains [94]. However, these associations are not always found and can differ in direction [95,96]. Environmental complexity may also impact brain size. The offspring of guppies taken from the wild and brought into captivity in the laboratory exhibit smaller brain sizes than their mothers, even in the first generation [97]. However, studies on whole brain size have been criticized, especially for neglecting regional specializations within the brain [98]. Some studies investigating the impact of environmental conditions on brain size in guppies have indeed found region-specific impacts and a lack of or much smaller change in whole brain size [95,97]. Additionally, investigating the size of the brain or brain components alone might lead to limited insight due to the multitude of other neurobiological mechanisms at play in the brain. Plastic shifts in connectivity between neurons or in circuit responsiveness may be particularly important in behavioural plasticity [99]. Thus, while understanding the causes and consequences of changes in brain volumes is important, these other neurobiological changes remain understudied in guppies and represent an exciting avenue for future research that will allow for a more precise understanding of the neurobiological underpinnings of behavioural plasticity.

(c) Genetic and epigenetic mechanisms

Investigating the genetic mechanisms underlying behavioural plasticity is key to understanding how plastic traits evolve and influence patterns of behavioural phenotypes seen in nature. Behavioural plasticity can differ between individuals and populations, and has been shown to evolve, suggesting a genetic basis [100]. In guppies, pedigree analyses have shown that behavioural propensities are heritable [40] but less is known about the heritability of behavioural plasticity. One study used pedigree analysis to investigate the genetic basis of behavioural plasticity in stress response traits and found that individual differences in behavioural plasticity were due in part to additive genetic effects [45]. Average behaviour in flight-type behavioural responses was also genetically correlated with plasticity, demonstrating genetic covariance between behavioural traits and behavioural plasticity. This is consistent with predictions that behavioural syndromes—suites of correlated behaviours expressed within or between contexts—may be composed of not only average behavioural responses, but also variation in behavioural plasticity [101]. If these average behaviours are correlated with differences in behavioural plasticity, genetic studies could investigate whether this correlation is due to a shared genetic architecture and what types of limits this correlation may impose on the evolution of behavioural plasticity. Available genomic resources, such as the reference guppy genome [10], offer opportunities to identify specific loci that are involved in the expression of behavioural plasticity, however, this will probably be challenging because behavioural traits are often highly polygenic [102].

New sequencing technologies have also enabled the evaluation of reaction norms via transcriptomics. High predation-origin female guppies exposed to predation exhibited shifts in brain oxytocin gene expression that were further modulated by social interactions [46]. Other studies have begun to characterize neurogenomic responses, cascades of rapid shifts in gene expression tied to specific stimuli, and have found that different mating contexts can induce considerable rewiring of co-expression networks in female guppies [44]. Additionally, patterns of gene expression in the brain have been shown to rapidly evolve following colonization of a low-predation environment [103]. How these shifts in gene expression are tied to changes in behaviour needs to be investigated. Future studies in guppies could investigate behaviour-associated plastic shifts in gene expression to help identify genes involved in behavioural plasticity. Plastic shifts in gene expression also suggest the potential involvement of epigenetic mechanisms, gene regulatory mechanisms that alter gene expression without altering the genetic code and could offer a direct link between the environment and the genome that underlies behavioural plasticity [104]. This could be investigated by examining contextual or developmental shifts in behaviour that are associated with shifts in gene expression and epigenetics such as DNA methylation or chromatin modifications.

5. Outstanding questions

Many questions in behavioural plasticity remain open, including several discussed above, and below we examine in detail three major questions that guppies may be used to answer.

(a) How do trait correlations and constraints influence behavioural plasticity?

One potential constraint is the interaction between different types of behavioural plasticity. Since guppies have been shown to respond to both current and past cues to express a range of types of behavioural plasticity, they are a useful system for investigating this constraint. Studies testing developmental or transgenerational plasticity should measure behaviours across different current contexts and cue exposures. For example, guppies could be used to investigate developmental behavioural plasticity in response to developmental predation stress, with individuals raised under varying developmental predation stress subsequently tested both with and without current predation cues. Past and current cues could be altered to investigate what happens when developmental cues are mismatched with the current environment. For example, Fischer *et al.* [105] reared fish from high- and low-predation environments in native and non-native environmental conditions and found behavioural variance increased and trait correlations shifted under non-native rearing environments. By giving mismatched cues in early development and adulthood and then testing for shifts in behaviour throughout adulthood, findings could provide information on the extent of irreversible developmental behavioural plasticity in guppies. Further, cue importance varies over a lifetime, so future studies investigating developmental and transgenerational behavioural plasticity could test across ontogeny to determine the stability of effects across age classes. Note that these types of behavioural plasticity may be overly dichotomized; many traits are probably on a continuum of being impacted by current versus past context.

(b) What ecological conditions favour the evolution of behavioural plasticity?

Theory suggests that phenotypic plasticity is favoured under five main conditions: (i) greater spatial and temporal environmental variation, (ii) higher dispersal, (iii) informative environmental cues, (iv) higher genetic variation for plasticity, and (v) lower costs/limits of plasticity [106]. However, few studies directly test these predictions. Owing to the variety of ecological contexts that guppies experience and their domestication, guppies provide a good system for testing these predictions using within-species, between-population comparisons. Theoretical predictions could be tested by sampling guppies from areas that differ in environmental variation and cue reliability (e.g. [107]). As previously mentioned, predation is variable between habitats, with some streams containing many co-occurring predators and some containing fewer [56]. One could predict that there will be increased levels of behavioural plasticity in guppies from more heterogeneous predation environments due to increased environmental variation. Guppies could be sampled from the corresponding habitat types and levels of behavioural plasticity could be assessed to test this prediction. Many laboratory populations of guppies derived from wild populations experience a great reduction in environmental variability. Levels of behavioural plasticity could be compared between laboratory populations and the wild populations that they originated from. However, care would need to be taken to ensure that genetic diversity is not limited in the laboratory populations as decreased genetic variation in plasticity may also have an impact. Moreover, one must isolate the effect of variability from changes in other factors, such as the absence of predation.

(c) What mechanisms underlie the expression and evolution of behavioural plasticity?

Within this broad question, one focus is particularly well suited for investigation using the guppy system—the identification of which brain regions and networks are involved in behavioural plasticity. Studying how brain regions with distinct functions change under varying ecological contexts could provide important insights into the role of brain expansion in mediating adaptive behavioural plasticity. Teleost fish have the unique ability to carry out extensive adult neurogenesis [8,99], allowing for rapid plastic changes within the neuroanatomy of the teleost brain in response to environmental factors on within-lifetime time scales. Many of the studies investigating this trait in fish have found region-specific shifts in size in response to environmental conditions such as social complexity [108], habitat complexity [109] and predation risk [110]. Depending on the type of behavioural plasticity or environmental condition being studied, different brain regions may be of interest. In guppies, the forebrain is implicated in learning responses to environmental changes, but the forebrain regions involved can be differentially activated depending on cue type (e.g. [33]). We suggest that guppy populations that differ in environmental conditions can be tested for differences in activity across brain regions and neural systems and levels of behavioural plasticity. This could be done using invasive populations that are experiencing new environmental conditions, laboratory populations exposed to various cues (e.g. alarm cue or parasite cues), or wild populations that differ in environmental conditions. Laboratory studies using overlapping cue exposures would be of particular interest. However, even focusing on brain region-specific changes is complicated by the likelihood that brain regions are involved in producing multiple behaviours and whole networks of brain regions may work together to produce single behaviours. Therefore, studies investigating the role of specific brain regions in behavioural plasticity will need to consider how these regions interact within networks.

6. Conclusion

While there is much to learn in behavioural plasticity research, especially regarding adaptive consequences, guppies have provided many important contributions to the field and represent a strong model for future research. Research using guppies has shown that predation impacts the level and nature of behavioural plasticity expressed and that behavioural plasticity may be an adaptive response to minimize the fitness impacts of ecological challenges such as parasitism and turbidity. Endocrinological studies using guppies have revealed that hormonal reaction norms can play a role in modulating the range of plastic responses, while neurobiological studies using guppies have shown a likely role for brain size expansion in behavioural plasticity. Genetic studies suggest there may be genetic covariance between behavioural traits and behavioural plasticity which could be an important constraint on the expression of behavioural plasticity. Investigating major outstanding questions using guppies as a model system will offer insights that will be informative for our understanding of behavioural plasticity across animals.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

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Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.A.F.: conceptualization, visualization, writing—original draft, writing—review and editing; M.W.T.: conceptualization, writing—original draft, writing—review and editing; A.H.: conceptualization, writing—review and editing; R.F.: conceptualization, visualization, writing—review and editing; S.M.R.: conceptualization, writing—review and editing; R.D.H.B.: conceptualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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