



Rapid shifts in behavioural traits during a recent fish invasion

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Abstract

Biological invasions are a prominent example of human-induced environmental change that pose a significant threat to worldwide biodiversity. Recent evidence suggests that behavioural traits play a key role in mediating invasion success. However, little research has investigated how rapidly behavioural traits can change during the initial stages of invasion. We investigated the influence of invasion on behaviour in a recent aquatic invader, the Siamese fighting fish (*Betta splendens*), in northern Australia. These fish represent a recent introduction (ca. 2010) and are thought to be descended from ornamental varieties released into the wild from the aquarium trade. Using fish reared under captive conditions, we measured differences in three ecologically relevant behaviours (activity, foraging, and aggression) across invasive and domestic fighting fish. We found that fish descended from the recent invasive population were more active and consumed fewer food items than their domestic counterparts. Furthermore, foraging latency was repeatable in invasive, but not domestic fish, and this seemed to be driven by an increase in among-individual variation in the invasive population. Finally, while we detected a positive relationship between activity and number of food items eaten in domestic fish, this relationship was absent in the invasive population, suggesting that invasion may have disrupted this behavioural syndrome. Our results highlight that invasion can alter ecologically important behavioural traits and behavioural syndromes, even during the initial stages of invasion, and emphasise the importance of incorporating behaviour into our understanding of invasion biology.

Significance statement

Alien species must rapidly adapt to novel environmental conditions in order to establish a successful invasive population. As behaviour mediates how organisms interact with their environment, behavioural traits may play a key role in facilitating invasion success. We investigated rapid changes in behavioural traits in a recently introduced (ca. 2010) ornamental fish, the Siamese fighting fish. We found that invasive fish differed from their domestic source population in two key behavioural traits—activity and foraging behaviour. Furthermore, we extend previous work by showing that invasion not only causes changes in average-level behavioural traits but can also result in changing patterns of behavioural variation and repeatability in newly established populations. Overall, our findings highlight that invasion can induce shifts in ecologically relevant behaviours, even during the early, crucial stages of invasion.

Keywords *Betta splendens* · Behavioural syndrome · Invasive species · Personality · Repeatability

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Introduction

Biological invasions are a leading cause of native species extinction (Clavero and García-Berthou 2005; Bellard et al. 2016) and cost the global economy billions of dollars (USD) per annum in management and mitigation (Pimentel et al. 2001; Hoffmann and Broadhurst 2016). Moreover, the frequency and magnitude of biological invasions are predicted to worsen with increasing globalisation, international trade, and a rapidly changing environment (Dukes and Mooney

1999; Levine and D'Antonio 2003; Westphal et al. 2008). Importantly, only a subset of species that are transported outside their native range establish a successful invasive population (Jeschke and Strayer 2005). With this in mind, identifying the traits that are selectively favoured in invasive populations—and hence how they may aid in invasion success—is of great environmental and economic concern.

Behavioural traits mediate how animals interact with their environment, and therefore, it is not surprising that behaviour plays a key role in facilitating invasion success (Sol et al. 2002; Rehage and Sih 2004; Rehage et al. 2005; Chapple et al. 2012). Previous research has shown that certain species exhibit behavioural traits that predispose them to successfully invade novel environments (Rehage and Sih 2004; Rehage et al. 2005; Chapple et al. 2011). For example, recent research comparing invasive and non-invasive lizard species, with an equal opportunity to invade, found that invasive species were more exploratory than non-invasive congeners (Chapple et al. 2011; Damas-Moreira et al. 2019). Such findings suggest that behavioural traits may play an important role in the ability of a species to successfully invade and become established in novel environments.

Furthermore, individuals within a single species often differ consistently in their behaviour (i.e. animal personality; Dingemanse and Réale 2005; Wolf and Weissing 2012). These personality traits (e.g. exploration, aggression, anti-predator behaviour) have been shown to be heritable (Dingemanse et al. 2002; Dochtermann et al. 2015) and may have important consequences for biological invasions. For example, founder effects may result in shifts in behavioural traits between native range source and invasive populations where behaviour mediates dispersal rates or the likelihood of survival in captivity and during transportation (Shine et al. 2011; Carrete et al. 2012; Chapple et al. 2012). Similarly, novel environmental conditions experienced in a species' introduced range may promote rapid evolution or phenotypic plasticity of behavioural traits within invasive populations (e.g. Pintor et al. 2008). For example, more recently established range-edge populations of the invasive round goby (*Neogobius melanostomus*) display increased boldness, activity, and dispersal rates when compared to individuals from longer-established range-core populations, and this may have evolved in situ due to spatial sorting of phenotypes at the range edge (Myles-Gonzalez et al. 2015; Thorlacius et al. 2015). Similarly, local ecological factors have been shown to mediate aggressive behaviour in multiple populations of signal crayfish (*Pacifastacus leniusculus*) throughout their invasive range (Pintor et al. 2008). Together, these results suggest that local conditions experienced throughout a species' invasive range may drive variation in behavioural traits that mediate invasion success.

Behavioural traits are often correlated with one another over time and across multiple contexts (i.e. behavioural

syndromes; Sih et al. 2004). For example, bolder individuals may also be more active and exploratory (Smith and Blumstein 2010) or more aggressive (Bell 2005). These syndromes can have important ecological and evolutionary consequences (Sih et al. 2004, 2012) and can, therefore, influence the success of biological invasions (Pintor et al. 2009; Chapple et al. 2012). Specifically, as different behavioural traits can be advantageous at various stages of the invasion process (i.e. introduction, establishment, spread etc.), any correlations between multiple behaviours that each promote success at different stages of invasion may facilitate colonisation success (Chapple et al. 2012). Furthermore, Pintor et al. (2009) demonstrated that a positive correlation between aggression and foraging behaviour may allow invasive crayfish to monopolise resources while maintaining high growth rates in their invasive range. Finally, local selection pressures may also influence behavioural syndromes. For example, exposure to predation generated a boldness-aggression syndrome in three-spined sticklebacks (*Gasterosteus aculeatus*; Bell and Sih 2007), suggesting that local selection pressures experienced in a species' invasive range may similarly drive variation in behavioural syndromes.

Interestingly, behavioural syndromes may also constrain local adaptation and, therefore, hinder invasion success. Where behavioural syndromes are the result of pleiotropic genetic effects (Ducrest et al. 2008; Aubin-Horth et al. 2012), behavioural traits may be prevented from reaching local optima within the invasive range (Sih et al. 2004). As an example, if foraging behaviour and activity were genetically correlated, selection for increased foraging behaviour during invasion may result in a correlated increase in activity, leading to increased predation and reduced invasion success. Selection may therefore favour the decoupling of behavioural syndromes during biological invasions where those syndromes constrain local adaptation. Despite the accumulating evidence for the importance of behavioural syndromes in mediating invasion success, there is still little empirical research documenting how behavioural syndromes change throughout the invasion process. Furthermore, among the few notable exceptions (e.g. Gruber et al. 2017a; Mueller et al. 2017; Magory Cohen et al. 2020), studies have tended to focus on well-established invasive populations, with little research documenting how behavioural traits change during the early stages of invasion.

Here, we investigated the influence of invasion on individual behaviours and behavioural correlations in the recently invasive Siamese fighting fish (*Betta splendens*). Siamese fighting fish are a small freshwater species native to South-East Asia and are popular in the aquarium trade—having been selectively bred since the Nineteenth century (Smith 1965; Jaroensutasinee and Jaroensutasinee 2001a). This species has recently (ca. 2010) been introduced to the Adelaide river floodplain (tropical monsoon climate) in the

Northern Territory, Australia, where it is rapidly spreading (Hammer et al. 2019). The invasive population is thought to be descended from ornamental aquarium fish released into the wild from the pet trade (Hammer et al. 2019). Interestingly, invasive fish now appear to be intermediate in morphology between artificially selected ornamental varieties from which they were descended, and wild type individuals (Hammer et al. 2019), suggesting rapid evolution or phenotypic plasticity of morphology after introduction to a novel environment. However, whether there is a similar divergence in behavioural traits remains to be tested. Previous research has reported that individual differences in activity and aggression can have important fitness consequences (Smith and Blumstein 2008; Moirón et al. 2019). We, therefore, investigated the differences in activity, foraging, and aggressive behaviour between recently invasive fighting fish and their domestic counterparts. Based on previous research finding that invasive populations are often more active and display increased foraging behaviour and aggression than their longer-established or non-invasive counterparts (e.g. Rehage et al. 2005; Groen et al. 2012; Myles-Gonzalez et al. 2015), we predicted an increase in activity, foraging, and aggressive behaviour in invasive, compared to domestic, fish. Furthermore, behavioural correlations can be strengthened (Chapple et al. 2012) or weakened (Sih et al. 2004) during invasions, and previous research has shown that behavioural syndromes can be altered by local selection pressures (Bell and Sih 2007). Therefore, while we did not have the requisite a priori knowledge to predict exactly how invasion would alter behavioural correlations in the Siamese fighting fish, we did expect that there would be differences in behavioural correlations between invasive and domestic fish.

Methods

Study species and animal husbandry

Domestic fighting fish used in this study (female: $n = 17$; male: $n = 19$) were captive-bred, ornamental varieties sourced from the aquarium trade (see supplementary material). Invasive fighting fish were originally collected from the Adelaide River (Northern Territory, Australia; 12.6603° S, 131.3361° E) in 2017. These wild fish were used to establish a stock population, where they were housed in large outdoor mesocosms (300 × 50 cm; diameter × depth; 3500 L; 44 fish per tank served as initial founders) for approximately 2 years (representing up to 4 overlapping generations) before taking part in the current experiment. Invasive fish (female: $n = 22$; male: $n = 17$) used in the current study were sourced from this stock population. Rearing fish under these captive conditions minimised potential differences in environmental effects on behaviour during development between

domestic and invasive fish. All animals were transported to Monash University, Australia, and housed in individual tanks (15 × 10 × 10 cm; water depth: 8 cm) filled with aged, carbon-filtered water (pH; mean ± SD = 7.66 ± 0.27) within a controlled-temperature room (12:12 h light:dark cycle) maintained at 24.5 °C. Fish were acclimated to laboratory conditions for at least 1 week prior to experiments. Individual housing tanks were oxygenated with an air stone and lined with 2 cm of a fine-pebble substrate. Fish were fed chironomid larvae ad libitum every second day.

Behavioural experiments

Domestic and invasive fighting fish were tested in three different behavioural assays. More specifically, fish performed (1) a maze assay (Fig. 1a), testing activity in a novel environment; (2) a foraging assay (Fig. 1b), testing foraging behaviour in a novel environment; and (3) an aggression assay with male fish only (Fig. 1c), testing aggressive behaviour directed towards a male conspecific. The three behavioural assays were tested in a fixed order with a 24-h gap between each—maze assay, foraging assay, and aggression assay, respectively—to reduce carryover effects (Bell 2013). All three assays were then repeated six days later to measure behavioural repeatability (Bell et al. 2009). Behavioural assays were all conducted in conditioned (i.e. Stress Coat treated; Aquarium Pharmaceuticals API®, Chalfont, PA, USA; 5 mL/38 L; e.g. D'Amore et al. 2019), aged, carbon-filtered freshwater from reservoirs maintained at 25.1 ± 1.1 °C. During the assays, fish were video recorded (Panasonic HC-V180) from above for later analysis. Videos were scored blind to experimental conditions. Upon completion of behavioural trials, each fish was photographed (Nikon DSLR D80 camera) for morphological analysis. Specifically, the standard length (i.e. snout to caudal peduncle) was measured using ImageJ software (Schneider et al. 2012).

Maze assay

All fish were tested for activity in a novel maze arena following previously established protocols for fish (Bertram et al. 2018; Martin et al. 2019). The maze arena (60 × 30 × 30 cm; water depth: 8 cm) was separated into six arms by five opaque white partitions (Fig. 1a). The arena was illuminated with white LED light strips (39 lx) placed around all 4 sides of the tank to better enable automated tracking software. The focal fish was initially confined to an acclimation area in the first arm of the maze (10 × 10 × 10 cm) for 5 min. At the start of the trial, a door to the acclimation area was removed remotely, and the fish was allowed to freely explore the maze for 10 min. Complete water changes were performed after every five trials. For the maze assay, we used the automated tracking software ToxTrac (Rodriguez et al. 2018) to record

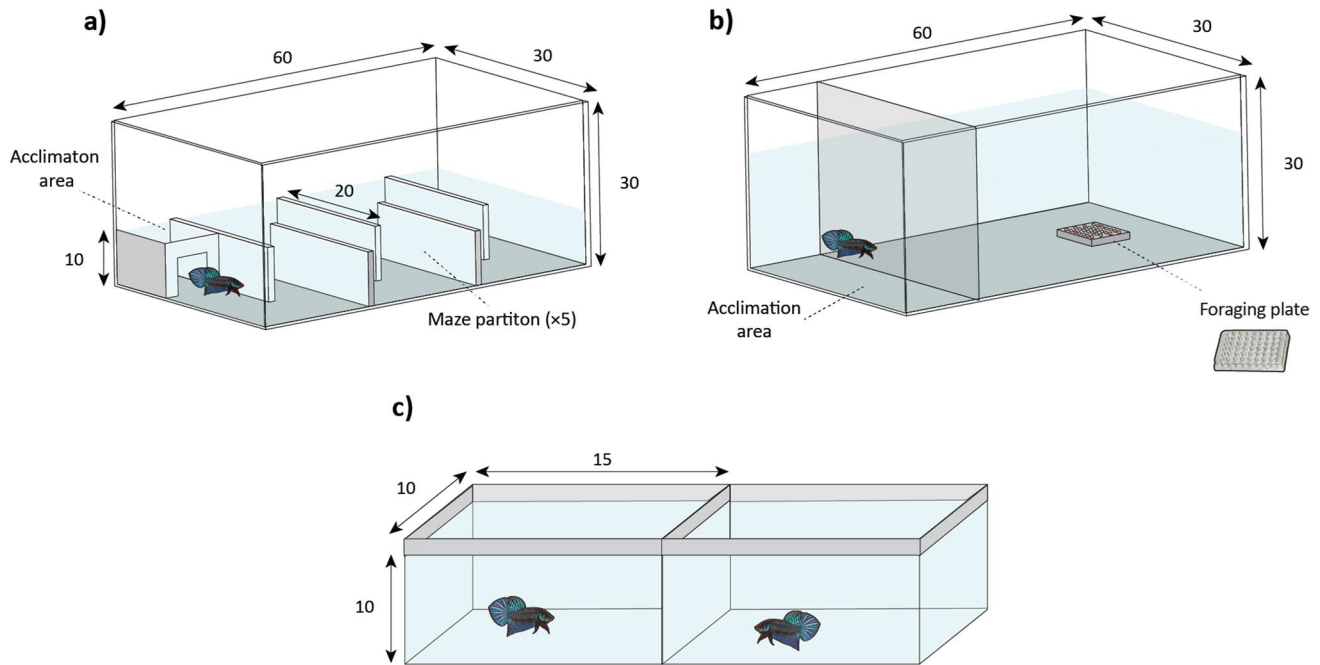


Fig. 1 Behavioural assays used to investigate **a** activity, **b** foraging, and **c** male aggressive behaviour towards a conspecific in both domestic and invasive Siamese fighting fish (*Betta splendens*; $n = 75$). All measurements are in centimetres

the average speed (mm s^{-1}) that the fish was moving during the assay as a measure of activity. A single maze assay of a domestic fish had to be discarded due to issues with automated tracking.

Foraging assay

Twenty-four hours after the maze assay, foraging behaviour was measured in a novel environment adapted from previously established protocols (Martin et al. 2019; Bertram et al. 2018). All fish were fasted for approximately 48 h before foraging trials to standardise hunger levels. Foraging arenas ($60 \times 30 \times 30$ cm) had a white sand substrate and were filled to a depth of 15 cm with water. Focal fish were initially confined to an acclimation area in the first 10 cm of the tank (Fig. 1b) for 5 min, using a transparent perforated partition. At the start of the assay, the partition was removed remotely, and animals were allowed to explore the foraging arena for 10 min. The foraging arena had a central ‘foraging zone’ (24×12 cm) 40 cm away from the acclimation area. The ‘foraging zone’ contained 64 shallow wells, in which twenty chironomid larvae (i.e. prey items) were randomly placed. The foraging arena, like the maze arena, was illuminated from the side with white LED light strips. Complete water changes were performed after every five trials. For each foraging assay, we manually scored the time to first strike at a prey item (i.e. foraging latency), and the number of prey items consumed. Fish that did not strike a prey item

during the assay were given a score of 600 s (i.e. the total duration of the assay).

Aggression assay (male fish only)

Male fish were tested for aggressive behaviour 24 h after the foraging assay, using a standard conspecific aggression assay (Verbeek et al. 2007). We chose to only record male aggressive behaviour as male fighting fish are highly aggressive and, since the 1800s, have been artificially selected for aggression and fighting ability (Smith 1965). All aggression assays were conducted in the males’ home tanks (Fig. 1c). On the morning of the aggression trials, all animals were fed three chironomid larvae to standardise hunger levels. For each trial, two male tanks were placed directly adjacent to each other. During the initial 5-min acclimation, visual contact between individuals was prevented with an opaque partition. At the beginning of each 10-min assay, the partition was removed, allowing visual contact between the two males. This design ensured that no animal was injured during the trials as fish never came into physical contact with one another. Fish were always partnered with a randomly chosen opponent from the same population but were paired with a different male for each trial (i.e. 2 different partners across the 2 trials). Male Siamese fighting fish engage in a range of stereotyped aggressive displays (Simpson 1968). Opercular gill flaring is one common aggressive behaviour in fighting fish and previous research has shown that the

frequency of gill flaring behaviour is positively related to contest outcome in male fish (Evans 1985). Therefore, during aggression assays, we recorded the number of opercular gill flares performed using the key-logging software BORIS (Friard and Gamba 2016).

Statistical analysis

Data were analysed using R version 3.6.0 (R Core Team 2019). Continuous covariates (i.e. length) were mean-centred prior to analysis to aid interpretation of model covariates. Foraging latency was log₁₀ transformed in order to approximate a Gaussian error distribution (Table S1). Both average speed and foraging latency were modelled using a Gaussian distribution. The number of food items eaten and the number of gill flares were analysed using a Poisson distribution (log link). Model assumptions were verified using diagnostic plots, and Poisson distributed models were checked for overdispersion.

First, behavioural repeatability was estimated separately for each population across all behavioural traits (i.e. activity, foraging latency, number of food items eaten, and number of gill flares). This was done using intra-class correlation coefficients from linear mixed-effects (LME) or generalised linear mixed-effects (GLM) models with behavioural traits included as a response variable and individual ID (i.e. 1–75) as a random effect (*rpt* function, *rptR* package; Stoffel et al. 2017). Specifically, repeatability was measured as the proportion of total behavioural variation that was attributable to among-individual variation. For Poisson distributed models, we report repeatability estimates on the latent (link) scale as suggested by Nakagawa and Schielzeth (2010). Ninety-five percent confidence intervals were calculated using parametric bootstrapping (1000 iterations), and the significance of repeatability estimates was determined using likelihood ratio tests (Nakagawa and Schielzeth 2010).

Second, mean differences in behavioural traits were compared across populations with LME or GLM models (*lmer* and *glmer* functions, *lme4* package; Bates et al. 2015) using each behavioural trait as the respective dependent variable (see Table S1 for model outputs). Models included the standard body length of the fish (mm) and trial number (one or two), as well as sex (male or female), population (domestic or invasive), and their interaction terms (sex × population) as covariates, while individual ID (i.e. 1–75) was included as a random effect. Furthermore, as water changes were conducted after every 5 trials, we included trial order with respect to the most recent water change (i.e. 1–5) to statistically control for any accumulation of conspecific cues in experimental tanks across the trials. Furthermore, as aggression assays were only conducted on male fish while in their home tanks, aggression models did not include sex or trial order with respect to the most recent water change as covariates. In addition, analysis of

aggression also included partner ID as a random effect. For all models, Wald tests were used to calculate the *P* values of fixed effects (*Anova* function, *car* package; Fox and Weisberg 2019).

Third, we investigated relationships between activity and foraging behaviour across populations using LME models (see Table S2 for selected models). Specifically, relationships between activity (maze assay) and both foraging latency and number of food items eaten were investigated separately across all fish (i.e. males and females). However, we did not investigate potential relationships between aggression and other behavioural traits due to limited statistical power as aggression was only measured in male fish. Both average speed and foraging latency were scaled (mean = 0, SD = 1) prior to analysis to aid in model fitting. All models included average speed as a response variable and either foraging latency or number of food items eaten as a predictor variable. Fish body length, sex, trial number, trial order, population, and a population × predictor behaviour interaction were also included as covariates. Individual ID was included in all models as a random effect to account for repeated measures. In these models, a statistically significant interaction term between population and the predictor behaviour would indicate a difference in the relationship between activity and foraging behaviour across the invasive and domestic populations (i.e. the relationship between the two behavioural traits differed by population). The *F* statistics were extracted from all LME models using Wald tests as described above. Relationships between behaviours within a single population were determined from model fixed-effects parameter estimates and test statistics using Satterthwaite's approximation for degrees of freedom (*lmerTest* package; Kuznetsova et al. 2017). Similar to Dhellemmes et al. (2020), we used LME models to quantify phenotypic correlations and were, therefore, required to take the 'individual gambit' and assume similar structure in covariances at the among- and within-individual levels (Brommer 2013). Advances in multivariate statistics have allowed the partitioning of phenotypic variation into both among- and within-individual components (Dingemanse and Dochtermann 2013). However, these approaches usually require larger sample sizes and greater repetition than was possible in the current study. Nevertheless, the approach employed in the current study allows a rigorous investigation of invasion induced variation in behavioural correlations in a recently invasive population.

Results

Repeatability

Both domestic and invasive fish demonstrated significant repeatability for activity, the number of food items eaten,

and aggression across trials (Table 1). However, foraging latency was only significantly repeatable in the invasive population (Table 1). This significant repeatability of foraging latency in the invasive population appears to be due to an increase in among-individual variation in invasive fish (Table 1).

Activity, foraging, and aggression

We detected a significant effect of population on activity, with invasive fish displaying increased average speed relative to their domestic counterparts ($F_{1,69} = 23.78$, $P < 0.001$; Fig. 2a). Furthermore, there was a significant main effect of trial with fish increasing their activity over time ($F_{1,73} = 7.78$, $P = 0.007$; Fig. S1a). However, for the foraging assay, we found no effect of population on the latency to first strike at a food item ($F_{1,69} = 1.67$, $P = 0.201$; Fig. 2b), but we did find a main effect of trial, with fish decreasing their strike latency over time regardless of population ($F_{1,74} = 35.74$, $P < 0.001$; Fig. S1b). In contrast to foraging latency, there were population differences in the number of food items eaten. Specifically, invasive fish ate significantly fewer food items than their domestic counterparts ($\chi^2 = 14.97$, $P < 0.001$; Fig. 2c). There was also a significant effect of trial, with fish increasing the number of food items eaten over time regardless of population ($\chi^2 = 9.76$, $P = 0.002$; Fig. S1c). However, there was no significant effect of sex, nor a sex by population interaction, on activity, foraging latency, or the number of food items eaten (Table S1). Finally, for the aggression assay, we found no population differences in the number of gill flares between male invasive and domestic fish ($\chi^2 = 0.62$, $P = 0.432$; Fig. 2d). However, we did find a main effect of length with larger fish displaying increased aggression relative to smaller conspecifics ($\chi^2 = 13.76$, $P < 0.001$; Fig. S2). Likewise, there was a main effect of trial, with fish decreasing their aggression over time ($\chi^2 = 10.22$, $P = 0.001$; Fig. S1d).

Table 1 Repeatability (R) and variance estimates (among and within) of both domestic and invasive fish for each behavioural trait. Note: repeatability for food items eaten and aggression were obtained from

Behaviour	Domestic		R (95% CI)	P	Invasive		R (95% CI)	P
	Among	Within			Among	Within		
Activity	35.92	15.18	0.703 (0.478, 0.836)	<0.001	19.18	16.90	0.532 (0.258, 0.723)	<0.001
Foraging latency	0.06	0.16	0.263 (0, 0.539)	0.064	0.29	0.17	0.631 (0.407, 0.787)	<0.001
Food items eaten	0.08	0.06	0.572 (0.297, 0.682)	<0.001	1.17	0.42	0.736 (0.519, 0.871)	<0.001
Aggression	3.72	0.68	0.846 (0.543, 0.956)	<0.001	1.19	0.48	0.712 (0.33, 0.881)	0.001

Behavioural correlations

For the model investigating the relationship between activity and foraging latency, there was no statistically significant interaction between the behavioural predictor variable (i.e. foraging latency) and population ($F_{1,127} = 0.03$, $P = 0.862$) indicating that the relationship between these traits did not differ among populations. However, we did find that the relationship between activity and number of food items eaten differed between invasive and domestic fish ($F_{1,141} = 4.66$, $P = 0.033$; Fig. 3). Specifically, for domestic fish, there was a statistically significant positive relationship, with more active individuals eating more food items ($t = 2.14$, $df = 141$, $P = 0.034$). However, there was no statistically significant relationship between activity and number of food items eaten for invasive fish ($t = -0.84$, $df = 140$, $P = 0.402$).

Discussion

We found that recently invasive Siamese fighting fish were more active, but consumed fewer food items, than their domestic counterparts. Furthermore, populations differed in the repeatability of their foraging behaviour. In particular, foraging latency was only significantly repeatable in the invasive, but not domestic population, and this seemed to be driven by an increase in among-individual variation in invasive fish. Additionally, after accounting for male size, invasive and domestic males did not differ in their aggressive behaviour. Finally, there were population differences in behavioural correlations. Specifically, domestic fish displayed a positive relationship between activity and number of food items eaten. However, there was no relationship between these behaviours in invasive fish.

In line with our hypothesis, invasive fish displayed increased activity in the maze assay compared to their domestic counterparts. Previous research has similarly reported increased activity in recently invasive populations and suggested that this may promote invasion success via increased likelihood of dispersal across the

GLM models using a Poisson distribution (log link) and estimates are reported on the link scale

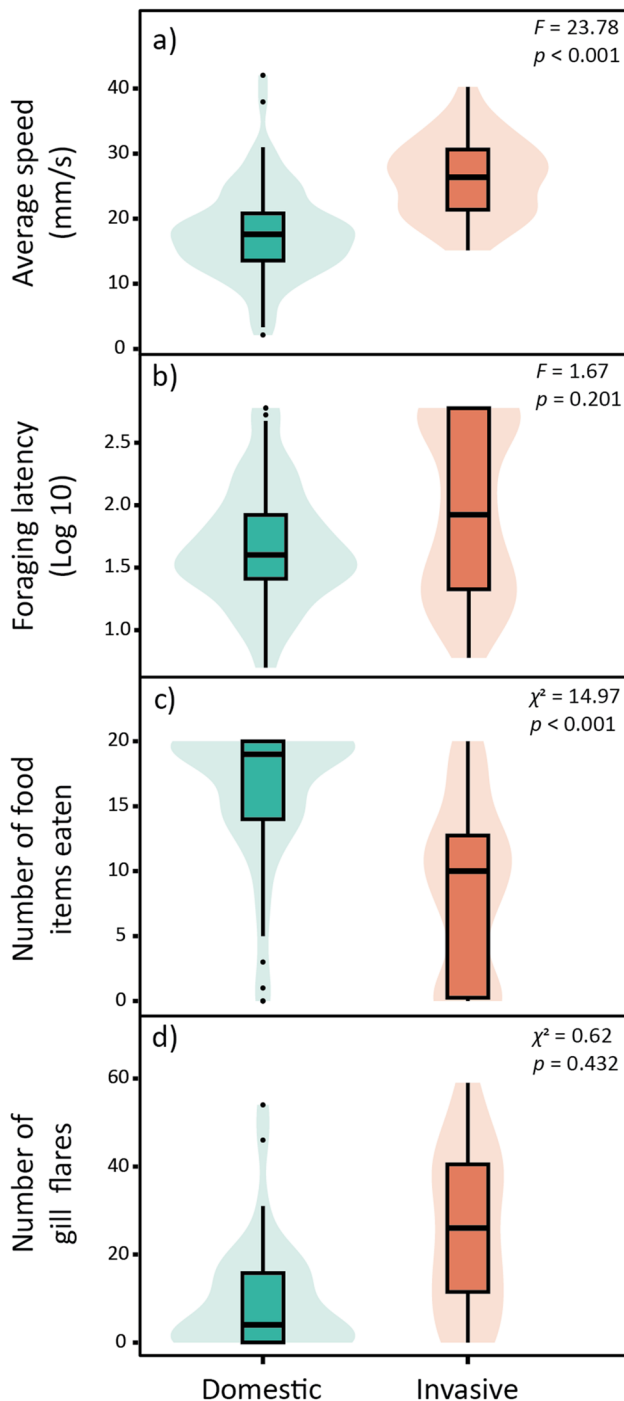
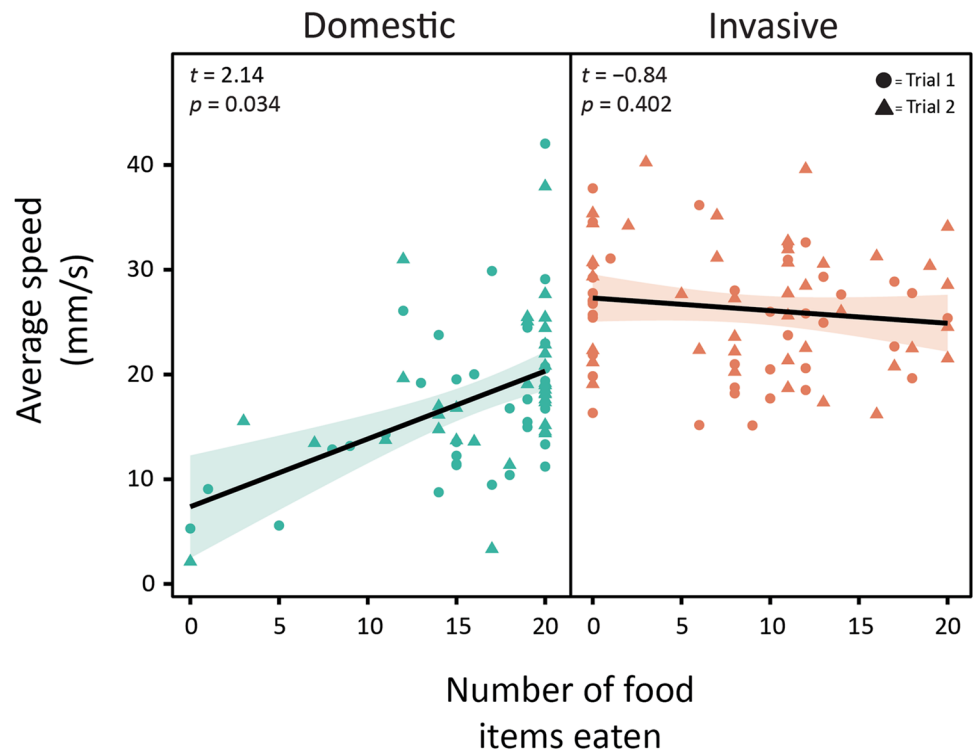


Fig. 2 Mean differences in behaviour across domestic ($n=36$) and invasive ($n=39$) Siamese fighting fish. Panels show population differences in behaviour for **a** activity, **b** foraging latency, **c** the number of food items eaten, and **d** aggression. For aggression trials, only male fish were tested (domestic $n=19$, and invasive $n=17$). Boxplots show 25th, 50th (i.e. median), 75th percentiles, and outliers. The shaded area surrounding the boxplot shows the probability density at different values smoothed by a kernel density estimator

invasive range (Myles-Gonzalez et al. 2015; Thorlacius et al. 2015). Furthermore, pre-establishment selection during deliberate invasions may bias behavioural traits in initial founder populations where there are associations between behaviour, survival in captivity, and likelihood of escape (Carrete et al. 2012). Indeed, previous research in the invasive yellow-crowned bishop (*Euplectes afer*) found that genotypes associated with reduced behavioural activity decreased in frequency over the initial stages of invasion (i.e. uptake and survival in captivity) and were less frequent in invasive, relative to native, range populations (Mueller et al. 2017). This suggests that selection during the initial stages of invasion may result in increased activity in newly invading populations. Furthermore, activity and exploration have been shown to vary across an invasive range (Myles-Gonzalez et al. 2015; Gruber et al. 2017b) and with environmental conditions experienced during development (Edenbrow and Croft 2013). Therefore, future research is needed to disentangle the contribution of spatial sorting, rapid evolution, or phenotypic plasticity to variation in activity in newly invasive fighting fish.

Contrary to our predictions, there were no differences in foraging latency between populations. Furthermore, we found that domestic fish ate significantly more food items than their invasive counterparts. These results are surprising and in contrast with previous research, which reported that invasive cane toads (*Rhinella marina*) displayed decreased foraging latencies when compared to native range conspecifics (Candler and Bernal 2015). Similarly, Damas-Moreira et al. (2020) found that invasive Italian wall lizards (*Podarcis siculus*) arrived sooner at food dishes and ate more food items than non-invasive congeners. However, invasive fighting fish may experience environments with higher quality food resources in the wild, relative to domestic conspecifics. These high-quality conditions may allow invasive fish to adaptively reduce their foraging effort relative to domestic populations while maintaining their energetic demands. Indeed, previous experimental evolutionary research in *Drosophila melanogaster* found that exposure to reduced diet quality over multiple generations can result in adaptive changes in foraging behaviour (Vijendravarma et al. 2012). This suggests that higher diet quality in the wild may explain reduced foraging behaviour in invasive fish compared to their domestic counterparts. Similarly, while there are constant opportunities to feed in the wild, aquarium trade fish are kept under more limited resource conditions where there may be increased competition for food. While these potential differences in resource availability between the populations were minimized by maintaining invasive fish under captive conditions, historic differences in feeding regime and resource availability may also explain the increased foraging behaviour seen in domestic fish.

Fig. 3 Across context behavioural correlation between activity and number of food items eaten from both trials in domestic ($n=36$) and invasive ($n=39$) Siamese fighting fish. The shaded area surrounding regression lines show SE



While we found no mean differences in foraging latencies between invasive and domestic fish, populations did differ in their repeatability and variance estimates. Much recent research has focused on the role of among- and within-individual variation in mediating how species adapt to environmental change (Fogarty et al. 2011; Snell-Rood 2013; Polverino et al. 2021). Indeed, as biological invasions consist of sequential ‘filters’ that can select for specific behavioural types, directional selection on behavioural traits during invasion is thought to result in reduced among-individual behavioural variation in newly invading populations (Chapelle et al. 2012). In contrast, we found that foraging latency was only significantly repeatable in the invasive population. This was largely driven by an increase in among-individual variation in invasive fish. As previous research has found that increased among-individual variation in behavioural traits may aid in the spread of invasive species (Fogarty et al. 2011), more research is needed to better understand the invasion history of Siamese fighting fish in northern Australia as well as the genotypic/phenotypic diversity present in the species invasive range. Furthermore, while we found differing variance estimates for foraging latency and a variety of other behavioural traits (Table 1), we advise some caution in interpreting these results due to the modest sample sizes, limited number of repeated trials conducted, and the use of only one invasive population. Future research with an increased number of repeated measures per individual with fish from multiple populations across their invasive range is needed to gain more robust parameter estimates and better

understand how invasion shapes behavioural variation in newly established populations.

We report no significant difference in aggression between invasive and domestic males. This is surprising considering previous research has documented increased aggression in invasive relative to native-range and long-established populations (Pintor et al. 2008; Groen et al. 2012), as well as differences in aggression between domestic and wild-type Siamese fighting fish (Verbeek et al. 2007). However, fighting fish are unusual among domesticated species in that they have historically been artificially selected for increased aggression and fighting ability (Smith 1965). Thus, invasive populations were likely already highly aggressive when introduced, providing limited potential for fish to become more aggressive during the invasion process. Furthermore, it is known that captivity may influence levels of intraspecific aggression (Price 1999). In the current study, we deliberately used captive-reared fish to minimise environmental differences that populations may experience during development. Here, it is possible that captive conditions may have resulted in reduced aggression. Therefore, it may be informative for future experiments to also compare aggression in newly caught, invasive fish to better understand how invasion may influence aggressive behaviour in this species. More generally, however, and in accordance with prior studies on male Siamese fighting fish (Jaroensutasinee and Jaroensutasinee 2001b), we found that larger males were more aggressive than smaller males, regardless of population. Relationships between size, aggression, and contest outcome have been

found in a variety of species (Arnott and Elwood 2009) and are thought to reflect size-dependent differences in resource holding potential and fighting ability (Maynard-Smith and Parker 1976). Furthermore, previous research in Siamese fighting fish has shown that male body size, display behaviour, and agonistic interactions can also play an important role in reproductive success (Doutrelant and McGregor 2000; Clotfelter et al. 2006). Whether invasion has altered these key mechanisms of sexual selection in invasive fighting fish remains an important topic for future research.

Finally, we found no population differences in the relationship between activity and foraging latency. However, there was a difference in the relationship between activity and the number of food items eaten between invasive and domestic populations. Specifically, there was a significant positive relationship between activity and the number of food items eaten in domestic but not invasive fish. Previous research has suggested that correlations between behaviours that each promote success at various stages of the invasion process (termed ‘invasion syndromes’) may increase invasion success (Chapple et al. 2012). Indeed, D’Amore et al. (2019) found that invasion promoted the formation of an exploration–aggression behavioural syndrome in swordtail fish (*Xiphophorus helleri-maculatus*) introduced to Hawaii via the aquarium trade. In contrast, invasive fish in the current study lacked the activity–foraging syndrome found in the domestic population. This suggests that there may have been weak or absent selection for a behavioural syndrome during the invasion of the species into northern Australia. While invasive fighting fish are thought to have been introduced from the aquarium trade (Hammer et al. 2019), it is not clear if these were intentionally released, or were escapees from ornamental fish ponds. Uncovering the invasion history of the species will, therefore, be needed to better understand how the invasive process may select for specific behavioural correlations in this recent aquatic invader. Furthermore, as behavioural syndromes may constrain local adaptation during biological invasions by preventing behavioural traits from reaching local optima (Sih et al. 2004; McGlothlin and Ketterson 2008), selective pressures in the invasive range may have favoured the decoupling of the activity–foraging syndrome in invasive fish. Additional research comparing wild and common–garden reared invasive fighting fish, using larger sample sizes, and an increased number of repeated measures with variance partitioning statistical approaches are needed to better understand how selection in the invasive range may have altered behavioural syndromes. Furthermore, many other ecological traits and interactions also remain to be studied in understanding the invasion, ongoing spread, and potential impacts of Siamese fighting fish in northern Australia.

In summary, we found that invasive fish were more active and consumed fewer food items than their domestic

counterparts. Furthermore, foraging latency was only significantly repeatable in invasive, but not domestic fish, and this seemed to be driven by an increase in among-individual variation in the invasive population. Similarly, there was a positive relationship between activity and the number of food items eaten in domestic, but not invasive fish. What the proximate causes of these behavioural shifts are, and whether they affect fitness, however, is unclear. Indeed, domestic and invasive fish were likely exposed to different conspecific densities, foraging conditions, and habitat complexity during ontogeny. As these developmental conditions have previously been shown to influence fish behaviour (e.g. Edenbrow and Croft 2013), future research on common garden–reared fish from multiple populations will be needed to disentangle the effects of phenotypic plasticity, spatial sorting, or rapid evolutionary change in driving behavioural change in this new invasive species. Taken together, these findings support previous research in suggesting that invasion can induce shifts in ecologically relevant behavioural traits, even during the early stages of invasion.

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Data availability Data is available in the Monash University online repository (10.26180/14463060).

Code availability Statistical code is available in the Monash University online repository (10.26180/14463060).

Declarations

Ethics approval Research was conducted in accordance with relevant Australian ethical guidelines and legislation and all procedures were approved by the Biological Sciences Animal Ethics Committee at Monash University (Ethics number: 21901).

Consent to participate Not applicable.

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Conflict of interest The authors declare no competing interests.

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