

Rapid divergence of animal personality and syndrome structure across an arid-aquatic habitat matrix

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Abstract Intraspecific trait variation, including animal personalities and behavioural syndromes, affects how individual animals and populations interact with their environment. Within-species behavioural variation is widespread across animal taxa, which has substantial and unexplored implications for the ecological and evolutionary processes of animals. Accordingly, we sought to investigate individual behavioural characteristics in several populations of a desert-dwelling fish, the Australian desert goby (*Chlamydogobius eremius*). We reared first generation offspring in a common garden to compare non-ontogenic divergence in behavioural phenotypes between genetically interconnected populations from contrasting habitats (isolated groundwater springs versus hydrologically variable river waterholes). Despite the genetic connectedness of populations, fish had divergent bold-exploratory traits associated with their source habitat. This demonstrates divergence in risk-taking traits as a rapid phenotypic response to ecological pressures in arid aquatic habitats: neophilia may be suppressed by increased predation pressure and elevated by high intraspecific competition. Correlations between personality traits also differed between spring and river fish. River populations showed correlations between dispersal and novel environment behaviours, revealing an adaptive behavioural syndrome (related to dispersal and exploration) that was not found in spring populations. This illustrates the adaptive significance of heritable

behavioural variation within and between populations, and their importance to animals persisting across contrasting habitats.

Keywords Boldness · Common garden · Dispersal · Exploration · Temperament

Introduction

Behavioural traits show patterns of variability across multiple ecological scales. Behaviour can vary within and between individuals, in addition to diverging among populations and species (Dingemanse et al. 2010; Sih et al. 2015). The discovery that intraspecific behavioural differences are common across animal taxa (Gosling 2001) has generated a renewed research focus on individual-level behaviour, particularly personality traits and behavioural syndromes (Reale et al. 2007; Sih et al. 2012). Personality (or temperament) traits are consistent and repeatable differences in behaviour between individuals (Reale et al. 2007; Wolf and Weissing 2012), whereas behavioural syndromes are correlations between functionally distinct personality traits within populations and species (Sih et al. 2004). While both personality traits and behavioural syndromes appear to be widespread in animals, how they function within an ecological and evolutionary context remains unresolved. A specific research focus is the potential for behavioural syndromes to constrain an individual's adaptive responses to ecological pressures and the implications of this for their evolutionary ecology (Sih et al. 2004; Dingemanse et al. 2007; Moya-Larano 2011). As individual differences in behavioural traits alter the nature of inter- and intraspecific ecological interactions, it has implications for a range of ecological fields including community ecology, environmental responses to

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anthropogenic change, and invasion ecology (Bolnick et al. 2011; Wolf and Weissing 2012; Wong and Candolin 2015). The integration of behavioural ecology into wider ecological and evolutionary theory should, therefore, be a priority of ecologists (Reale et al. 2007).

The study of personality has traditionally been centred on human psychology, but its recent application in ecology requires that personality traits adopt ecologically relevant definitions (Sih et al. 2004). Core categories, including boldness, exploration, activity, sociability and aggression, are derived from the context in which they are measured (Reale et al. 2007). However, the inconsistent terminology and methodology used to define each trait is a major barrier to integrating individual behavioural ecology into wider ecological theory (Reale et al. 2007; White et al. 2013). For example, boldness traits can be defined as the tendency to undertake risky behaviour (Wilson et al. 1994), such as responses to predators, novel environments or novel objects (Dingemanse et al. 2007; Chapman et al. 2010, 2011). An alternate approach suggests responses to novelty should be described as exploratory traits (Reale et al. 2007). Despite data showing bold-exploratory behaviours are correlated with each other (Brown et al. 2007b), studies of damselfish (*Pomacentrus* spp.) found common measures of boldness-exploration were not interchangeable and could diverge independently (Beckmann and Biro 2013; White et al. 2013). Intriguingly, only one bold-exploratory trait in damselfish—the distance ventured from a shelter—had implications for their survival when exposed to predation. Further studies have found that boldness traits can be associated with dispersal (Chapman et al. 2011), diet (Chapman et al. 2010; Rockwell et al. 2012), foraging range or method (Jolles et al. 2013; Patrick and Weimerskirch 2014), and social role (Bergmüller and Taborsky 2010; Keiser and Pruitt 2014). Currently, our ability to create an ecologically relevant framework for animal personality is somewhat limited by the lack of empirical studies showing how traits respond to various ecological pressures.

A common garden framework allows personality traits to be assessed without the influence of ontogenic effects, i.e., environmental effects within the animal's lifetime (Herczeg et al. 2009; Miranda et al. 2013). Environmental factors can alter personality phenotypes in individuals, as shown in field crickets (*Gryllus texensis*), which were less exploratory and increasingly sought shelter following an encounter with a predator (Adamo et al. 2013). Similarly, bluefin killifish (*Lucania goodie*) raised in a low food environment had more aggressive personalities than those raised in high food environments (McGhee and Travis 2011). Contrastingly, inherent non-ontogenic personality divergence may be the result of natural selection, as behavioural phenotypes can show varying degrees of heritability (van Oers et al. 2004; Brown et al. 2007a) and a single personality trait is likely

to be associated with multiple genes and genomic regions (van Oers and Mueller 2010). Transgenerational epigenetic and maternal effects also have the potential to influence the behavioural phenotype of the F1-generation offspring raised within a common environment (Buss and Greiling 1999; Herczeg et al. 2009). Thus, this approach has been recently used to analyse the response of personality phenotypes to anthropogenic change and predation pressure (Herczeg et al. 2009; Miranda et al. 2013), to explore the relationship between ecological pressures and consistent inherent phenotypic differences in behaviour.

Studying phenotypic divergence across multiple personality traits is useful to explore the influence of behavioural syndromes on ecological interactions and the evolution of individual differences. Syndromes theoretically alter the mechanics of individual adaptive responses to environmental stressors (Sih et al. 2004). The constraint hypothesis proposes that rigid personality types and proximate mechanisms underlying behavioural traits, such as hormonal or pleiotropic gene processes that underpin multiple traits, may inhibit an animal's optimal behavioural response to environmental conditions (McGlothlin and Ketterson 2008; van Oers and Mueller 2010; Adriaenssens and Johnsson 2013). The adaptive hypothesis instead suggests that behavioural correlations should only arise where selection favours covariance between traits (Dingemanse et al. 2007; Moya-Larano 2011). In three-spined sticklebacks (*Gasterosteus aculeatus*), wild populations from large ponds with predatory fish present showed an aggression-exploratory-activity syndrome. By contrast, populations from small, predator-free ponds showed no such correlation, suggesting the syndrome is adaptive (Dingemanse et al. 2007). As these were wild populations, the divergence may be the result of learned behaviours, trait-based selection during early life stages or survival bottlenecks, all of which can generate syndromes (Bell and Sih 2007; Adriaenssens and Johnsson 2013). Nonetheless, Bell (2005) found differences in heritability of syndromes between two stickleback populations, suggesting the syndrome is adaptive. Studying how contrasting ecological pressures affect inherent behavioural syndromes allows us to investigate where they are acting as a constraint, or as a result of adaptive responses, and explore the implications for the evolution of individual behaviour.

The Australian desert goby (*Chlamydogobius eremius*) is a small (6–8 cm maximum length) desert dwelling fish that show personality divergence between wild populations associated with habitat (Moran et al. 2016). Gobies occupy two distinctly different aquatic habitats with contrasting ecological stressors in arid Australia (Thompson and Withers 2002; McNeil et al. 2011). First, Great Artesian Basin (GAB) forms isolated groundwater-fed spring habitats where the goby is likely to experience intense resource competition in the absence of aquatic predators (Murphy et al. 2012;

Davis et al. 2013). In contrast, Lake Eyre Basin (LEB) surface water rivers show extreme hydrological variability, are largely ephemeral and have more diverse fish communities including larger aquatic predators (Kotwicki and Allan 1998; McNeil et al. 2011). Wild populations show higher boldness and reduced activity in spring versus river populations, suggesting personality traits are being influenced by the differing ecological pressures within each habitat type (Moran et al. 2016). Despite this divergence, sporadic floods can provide dispersal pathways for the desert goby across this arid–aquatic habitat matrix, such that springs and river populations are not genetically differentiated (Mossop et al. 2015).

To further explore this personality divergence and the mechanisms underlying it, we sought to determine if gobies reared in a common garden show similar trait differences to their wild populations. This focused on bold-exploratory traits, as these have been shown to be associated with competitive and predation pressure (Chapman et al. 2010; Rockwell et al. 2012; Patrick and Weimerskirch 2014). Larger scale movement behaviours, i.e. dispersal, were also included as studies have linked bold-exploratory traits and dispersal in other fish taxa (Cote et al. 2010a; Chapman et al. 2011), and these behaviours are particularly relevant to desert gobies considering the species' large range and occupancy of ephemeral habitats (Mossop et al. 2015). Finally, to explore potential syndrome divergence we examined if correlations between personality traits differ between gobies between spring and river populations.

Methods

Laboratory reared fish used for this study were first-generation offspring of wild populations, which were collected from two artesian springs and two riverine waterholes (Fig. 1). Despite limited replication across habitat types in this study, previous research has established that these habitat differences are associated personality trait divergence in wild goby populations (Moran et al. 2016). Across three spring and three river sites (including the four current study sites), this showed wild spring populations to have elevated boldness in a novel food item context and reduced activity in a novel environment context. Since a population's genetic context can be relevant for understanding the distribution of behavioural variation (e.g. Wong et al. 2004), we employed the framework provided by Mossop et al. (2015), who used allozyme and mitochondrial DNA data to elucidate the desert goby's population genetic structuring and identify the presence of two main genetic groups—Northern and Southern—in the north and south of the species' range, respectively (Fig. 1). These results suggest that genetic structuring of populations principally diverges between

catchments connecting to either the north or south lagoons of Lake Eyre (Mossop et al. 2015). We note that one such population (the Bubbler) was characterised with sequences of the Cytochrome *b* gene (GenBank accession numbers KP146114, KP146115, KP146120), which are described in Mossop et al. (2017). However, methods for the preparation and analysis of all molecular data including the Bubbler are provided by Mossop et al. (2015). In the current study, populations from both spring and river habitats were sourced from south lagoon catchments to avoid genetic confounds. Importantly, these desert goby populations appear to show gene flow sufficient to prevent genetic differentiation, consistent with the recent or ongoing connectivity of habitat types (Mossop et al. 2015). This suggests that any inherent (i.e. non-ontogenic) behavioural divergence seen between populations is the result of either contemporary selection or epigenetic/maternal effects (Herczeg et al. 2009; van Oers and Mueller 2010).

Collection of wild fish used consistent methodology to avoid personality-biased sampling (Michelangeli et al. 2015), using a combination of hand dip nets and box traps (30 × 20 × 20 cm, 2" aperture, mesh size 1 mm, SureCatch, Singapore). As described in Moran et al. (2016), a maximum of 50 fish per site were sampled in March–April (autumn) and transported to Monash University according to previous published methods (Wong and Svensson 2009) and housed in large stock aquaria (80–110 L). Gobies readily breed in a laboratory environment, so egg clutches were drawn from both stock aquaria housing wild gobies (adult males and females) and smaller tanks subdivided into compartments for housing male–female breeding pairs. Housing tanks included a layer of 2 mm gravel substrate, artificial aquarium plants and nesting sites (PVC piping and halved terracotta pots, eight per stock tank or one per breeding pair compartment).

Nesting sites containing egg clutches were collected by hand and placed into small hatching tanks (20 × 30 cm, 10 cm depth, 1–2 clutches per tank). Although direct parentage was not tracked from wild to F1 experimental fish, 4–5 clutches with distinct parentage were hatched from each population to limit the influence of potential clutch effects (Mousseau and Fox 1998; Carere et al. 2005). When juveniles reached approximately 1.5 cm in length, 24 experimental fish per population (approximately 50:50 sex ratio) were selected at random from hatching tanks and placed into four rearing tanks. Rearing tanks were subdivided by partially permeable barriers into sections (12.5 × 45 cm, 30 cm depth) which housed six individuals per population to control for density effects. Populations were randomly allocated to a different compartment in each of the four rearing tanks. This common garden approach accounts for the effects of minor differences between tank conditions so that behavioural divergence could be attributed to population or

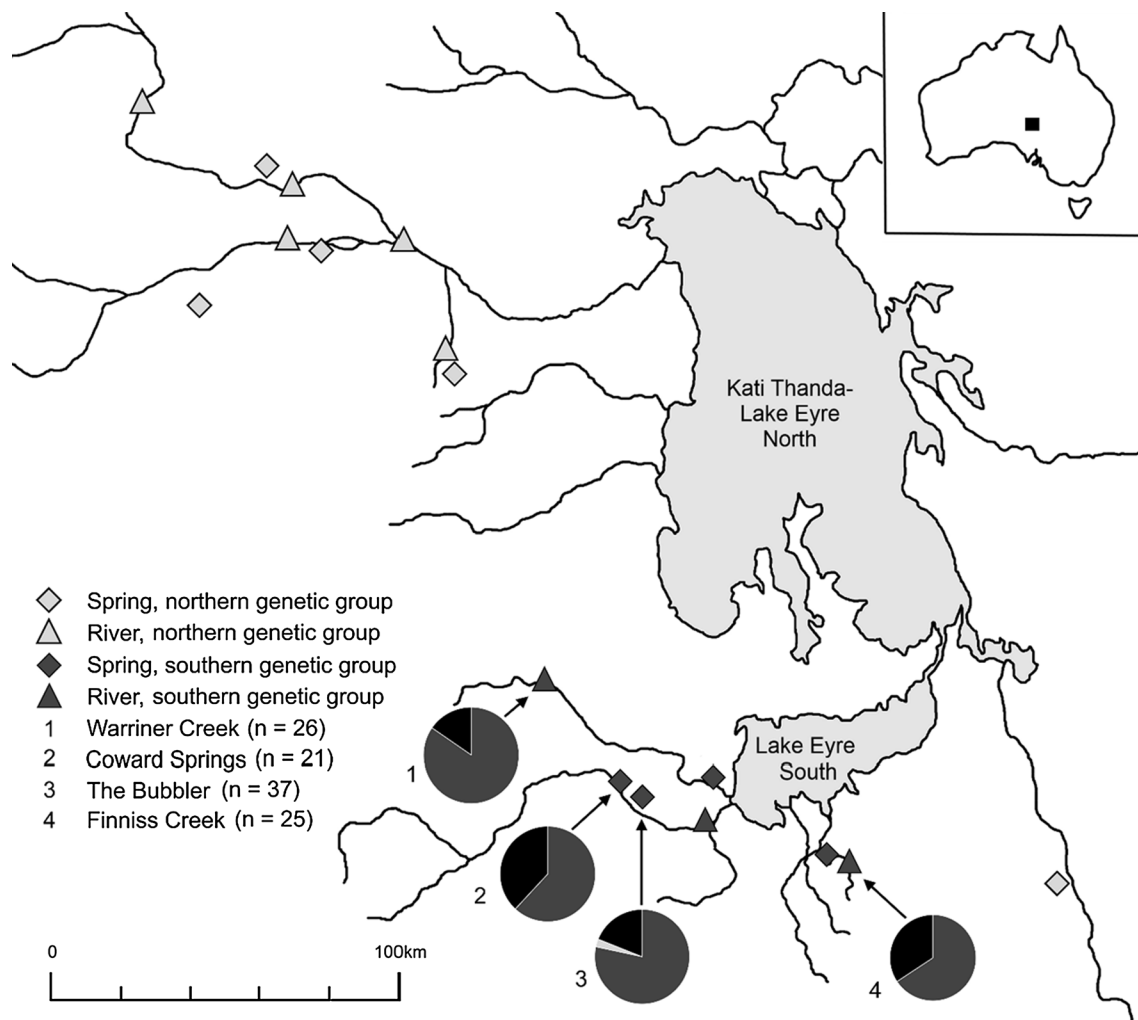


Fig. 1 Phylogeographic structure is evident within the desert goby (*Chlamydogobius eremius*; Mossop et al. 2015): a northern genetic group (light grey triangles and diamonds) and a southern genetic group (dark grey triangles and diamonds) are present. The four current study sites fall within the southern genetic group. For each population, pie charts indicate the relative frequencies of haplotype 1 (characteristic of the southern group;

dark grey), haplotype 2 (characteristic of the northern group; light grey) and all other haplotypes (black, after Mossop et al. 2015), although data for The Bubbler are new. The sites included two springs: the Bubbler ($-29.446483^{\circ}/136.857849^{\circ}$) and Coward Springs ($-29.400388^{\circ}/136.794193^{\circ}$); and two river waterholes: Warriner Creek ($-29.137986^{\circ}/136.568422^{\circ}$) and Finnis Creek ($-29.610250^{\circ}/137.458289^{\circ}$)

habitat differences between experimental groups (O'Steen et al. 2002; Relyea 2002). Fish were maintained in controlled conditions in both the rearing tanks and experimental assays (10.0 ± 0.5 mS/cm, 25 ± 1 °C, 12:12 h light:dark cycle), with a standard diet (Otohime EP1 1.5 mm hirame pellet and C1 0.58–0.84 mm granule, Marubeni Nisshin Feed Co. Ltd., Japan). These water conditions were chosen as a range of goby populations have readily adapted to these conditions in our experience. These parameters also fall in the intermediate range of temperature and salinity across sites at sampling, which can differ, particularly at river sites which can have extremely high variability in temperature, salinity and turbidity depending on flow conditions (see Moran et al. 2016). Fish were subject to multiple assays upon becoming

sexually mature adults, defined as fish greater than 4 cm in total length, as nuptial coloration of males suggests that experimental fish were sexually mature at this length (Svensson et al. 2010).

Behavioural experiments

Three behavioural assays followed previously published methods (Moran et al. 2016), under the same physical conditions as the fish were housed in. On day 1, individuals randomly selected ($n = 88$) from rearing tanks were isolated in a 3-L 'home tank' ($10 \times 25 \times 20$ cm). Fish undertook dispersal and exploration assays on days 2 and 3 in random order to account for carryover effects (Dochtermann 2010;

Bell 2013). Fish undertook a novel food item assay on day 10, after other trials. This gave fish an extended acclimation period in their 3 L home tank so that novel item responses were not conflated with novel environment responses. At least ten individuals per population undertook these assays again 4 weeks after the initial trials, to assess which variables show consistent intraspecific differences and constitute personality traits (Herde and Eccard 2013).

Novel environment assay

Individuals were placed in a 15 × 15 cm enclosed refuge at one corner of a 75 × 45 cm tank. The tank is subdivided into five 15 cm corridors by opaque white barriers (to match the walls of the tank), and the entire area is subdivided into 5 × 5 cm grid squares. The novel tank is filled to a 10-cm depth, which is drained, rinsed with reverse osmosis water and refilled between trials to avoid chemical cues carrying over between trials. After a 15-min acclimation, the refuge door (7.5 × 4 cm) was opened remotely. From the time that fish completely emerge from the refuge, individuals are given 10 min to explore the novel environment. Latency to emerge into the novel environment was recorded as a possible measure of boldness, analogous with the common ‘open field paradigm’ based on an individual leaving a refuge space into an open unknown space, which can potentially be associated with bold or exploratory traits (Brown et al. 2007b; Burns 2008; Chapman et al. 2011). Fish that did not emerge within 15 min ($n = 4$) were given the maximum score (900 s), similar to the approach of Brown and Irving (2014). Variables collected during the 10-min exploration period were activity level (grid squares entered per second), area explored (total number of grid squares entered), latency to reach the endpoint (i.e. the opposite corner of the tank) and the use of maze edges (the ratio of wall-adjacent to non-wall-adjacent grid squares entered). Observations were made remotely, via two CCTV cameras located 1 m above the novel tank, to eliminate human observer effects on behaviour.

Dispersal assay

To test larger scale movement and exploratory behaviours, individual fish were introduced to a dispersal assay, as described in Mossop et al. (2017) and modelled off similar experiments for other fish species (Rehage and Sih 2004). A focal fish was placed in the topmost pool of a series of four cascading pools (127 × 84 cm, filled to an approximately 15 cm depth), linked by one-way riffle channels (1 m long with a minimum depth of 2 cm). Pools were filled with a layer of 2 mm gravel, six identical plastic aquarium plants and six halved ceramic pots for refuge, such that the apparatus mimicked shallow interconnected pools commonly

encountered by gobies in both spring and river habitats. The system recirculated with a flow averaging 370.4 mL/s via an inline pump (Heto Brand, Hengtong Aquarium Co., Ltd. Guangdong, China). Fish were acclimated to the novel environment and flow rate in the top tank for 40 min, with a water permeable barrier preventing dispersal. Trials were initiated by removing the barrier. Fish were given 3 h to disperse. Key variables recorded were distance dispersed (in number of pools the fish travelled down the one-way system) and whether fish reached the endpoint of the dispersal assay.

Novel item assay

In their individual home tank, fish were presented with a food item they had not previously encountered, i.e. a 0.1-g cube of lamb liver. Opaque partitions were placed around three sides of the tank 30 min before the trial. The item was dropped at open end of the tank using 25 cm forceps, where a camera (Canon Powershot S100 Digital Camera) was positioned at the open end of the tank to observe behaviour. Filming began 5 min before the trial was initiated to limit observer effects due to turning on the camera. Fish were allowed 5 min to inspect (i.e. actively swim within 2.5 cm of the item) and attempt to feed on the novel item. Key variables were latency to inspect the novel item and latency to feed on the item, as common measures of bold-exploratory personality traits (Dingemanse et al. 2007).

Statistical analysis

All statistical analyses were conducted using the R Statistical Package 3.1.2 (R Core Team 2014). Repeatability was initially assessed using Spearman’s Rank Correlations between the first and second trial scores of all fish with repeat trials, as a non-parametric test to establish significant ($\alpha < 0.05$) behavioural consistency within individual fish for each variable (Brown and Irving 2014). Repeatable variables were used for subsequent analysis, so were checked for normality (Shapiro–Wilks) and where necessary transformed to either a Gaussian or binomial distribution (Table 1). Binomial datasets were transformed from raw data as 1 (latency < median score) or 0 (latency > median score), similar to Brown et al. (2007b). To maximise comparability with other studies and between each variable, additional estimates of repeatability with confidence intervals (95%) were produced for transformed variables (‘rptR’ package, Nakagawa and Schielzeth 2010). Both non-adjusted and population-adjusted repeatability estimates were calculated using a linear mixed effect model (LMM) approach for Gaussian and a generalized linear mixed effect model (GLMM) approach for binomial variables, as these readily account for confounding factors (Table 1).

Table 1 Key behavioural variables, only including variables that showed significant repeatability using a Spearman's rank correlation (ρ)

Variable	Assay	Distribution	Spearman's ρ	Repeatability estimates	
				Raw	Adjusted
Activity ^a	Novel environment	Normal	0.597 ($P < 0.0001$)	0.303 (0.096, 0.495)	0.407 (0.129, 0.616)
Edge use ^b	Novel environment	Normalized with $\ln(1 + x)$ transformation	0.420 ($P = 0.0046$)	0.238 (0.031, 0.417)	0.331 (0.045, 0.573)
Maze endpoint latency ^c	Novel environment	Bimodal, converted to binomial	0.319 ($P = 0.0348$)	0.025 (0, 0.217)	0.033 (0, 0.304)
Inspection latency ^d	Novel item	Bimodal, converted to binomial	0.734 ($P < 0.0001$)	0.171 (0, 0.209)	0.185 (0, 0.421)
Feeding latency ^e	Novel item	Bimodal, converted to binomial	0.525 ($P = 0.0014$)	0.188 (0, 0.742)	0.295 (0, 0.852)
Dispersal distance ^f	Dispersal	Bimodal, dispersal endpoint used from further analysis	0.397 ($P = 0.0063$)	–	–
Dispersal endpoint reached ^g	Dispersal	Binomial	0.420 ($P = 0.0036$)	0.405 (0.046, 0.941)	0.422 (0.027, 0.896)

^aThe total number of times a fish entered a grid square within the novel environment, per second that the fish was within the novel environment. A fish was deemed to have entered a grid square when >50% of its body was within the square

^bTo quantify how much an individual clung to the maze walls, the ratio of squares in the centre of corridors entered (out of 39 central squares) to squares at the sides of corridors entered (out of 78 edge squares) was calculated. The final nine square maze segment was excluded as this section has an increased ratio of edge to central squares, so would negatively bias fish that reached the final segment

^cTime taken to reach the end row of grid squares in the final corridor of the novel maze, measured from the time that the individual first emerges from the refuge. Maximum latency is set to 600 s

^dTime taken for the focal fish to actively swim to within 2.5 cm of the novel food item. If the novel food item was dropped within 2.5 cm of the fish, time taken for the fish to then begin actively swimming towards the food item was used. Maximum latency is set at 300 s

^eTime taken for the focal fish to attempt to feed on the novel food item. Maximum latency is set at 300 s

^fThe distance that the fish moves down the dispersal assay within a 3-h period, measured in number of pools, from 0 (no dispersal) to 3 (complete dispersal)

^gA binomial measure of dispersal tendency, with 0 = no or incomplete dispersal and 1 = complete dispersal within 3 h

The effects of habitat, sex and total fish length on normally distributed variables (activity, edge use) were tested using LMMs with habitat and sex as predictor variables nested within population, and length as a continuous covariate ('lme4' package, Bates et al. 2014). General linear hypothesis tests ('glht' function) with Tukey contrasts were used to test the significance of habitat and sex effects, whereas non-zero 95% confidence intervals were used to determine the length covariate effects. A similar approach was used for inspection latency, feeding latency, maze endpoint latency and dispersal endpoint variables, instead employing GLMMs (Bolker et al. 2009).

These effects were further investigated by entering untransformed data for all repeatable variables into a 'rda' redundancy analysis ('vegan' package, Oksanen et al. 2015). Habitat, sex and length effects associated with the PC1 and PC2 variables were analysed using linear models. Relationships between each variable and the potential presence of behavioural syndromes were investigated using Pearson product-moment correlations (Evans et al. 2010; Adriaenssens and Johnsson 2013). Strong behavioural divergence between spring and river populations suggests that these populations are subject to distinctly different ecological pressures in each of these habitats; therefore,

Pearson correlations were conducted for spring and river fish separately.

Results

Repeatability showing consistent intraspecific variability in the behavioural responses of gobies was found in seven variables from across all assays (Table 1). In the novel environment assay, fish habitat type, sex and length were associated with multiple variables (Fig. 2). Specifically, spring fish had lower activity (effect size = -0.1633 , $Z = -2.479$, $P = 0.0132$) and used the edges of the maze less than river fish (effect size = 0.1079 , $Z = 3.007$, $P = 0.0026$). Male fish had lower activity (effect size = -0.1769 , $Z = -2.479$, $P = 0.0132$), but used the edges of the maze more than female fish (effect size = -0.0631 , $Z = -3.466$, $P = 0.0005$). Larger fish had higher activity [effect size = 0.0969 , 95% CI (0.0223, 0.1714)] and used maze edges less [effect size = 0.0366 , 95% CI (0.0178, 0.0565)]. There was no effect of sex, length or habitat on latency to reach the maze endpoint. In the novel item assay, spring fish were quicker to both inspect ($Z = 4.055$, $P < 0.0001$) and attempt to feed ($Z = 4.049$, $P < 0.0001$) on the novel food item (Fig. 3).

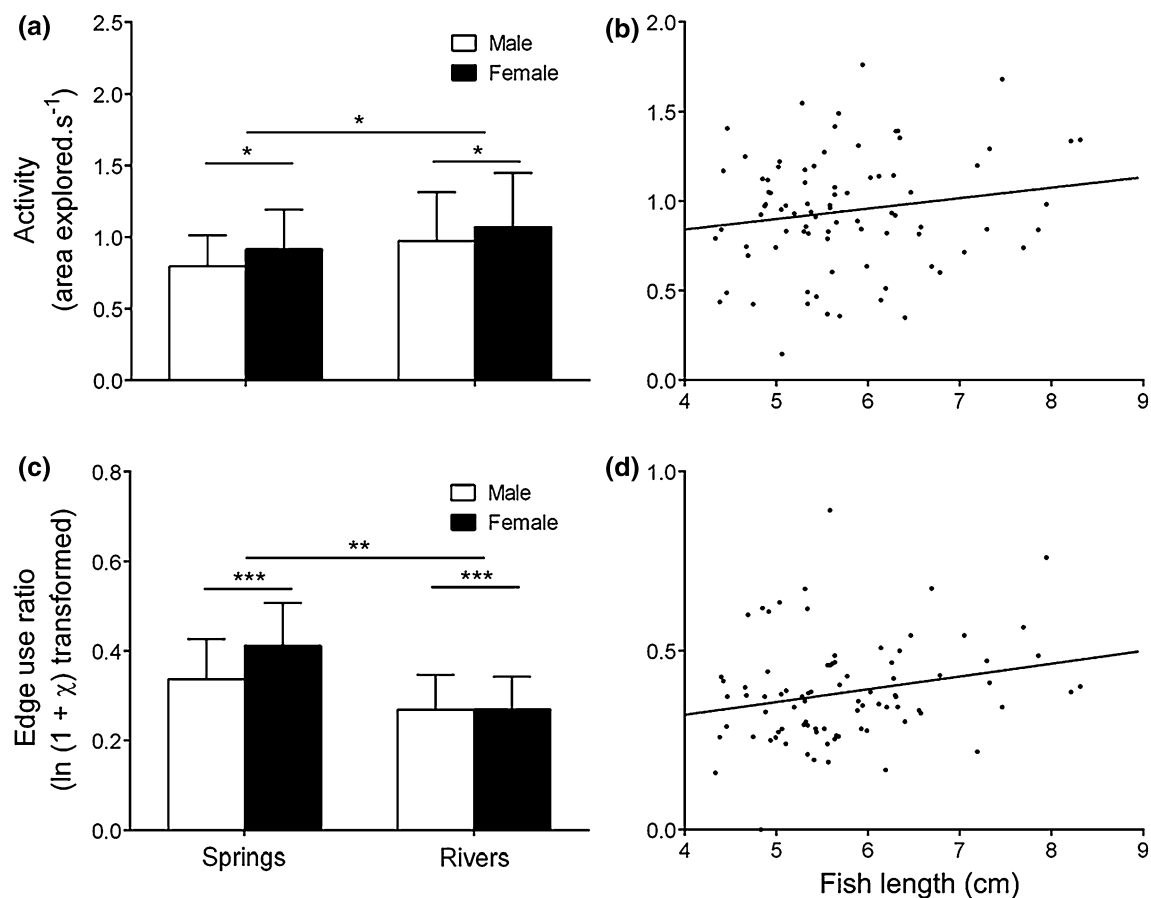


Fig. 2 Behavioural variability in novel environment trials, including the effects on an individual's activity score from **a** habitat, sex and **b** length, and the effects on their edge use from **c** habitat, sex and **d** length ($n = 84$). Error bars = 1 standard deviation

There was no significant effect of sex and length on these variables. Within the dispersal assay, there was no significant effect of sex, length or habitat on fish reaching the dispersal endpoint.

Redundancy analysis resolved the seven repeatable variables into the combined variables, PC1 and PC2 (eigenvalues = 2.296, 2.151, respectively), explaining 63.53% of the variability in the seven input variables (Fig. 4). Linear models showed that spring individuals were significantly different from river individuals on PC1 ($F_{1,62} = 9.711$, $P = 0.0028$) and PC2 ($F_{1,62} = 25.67$, $P < 0.0001$), suggesting at least two distinct axes of behavioural divergence across three assays. There was no significant effect of sex or length on PC1 or PC2, suggesting that habitat is the principal driver of behavioural divergence on these axes. Component loadings showed that PC1 was primarily associated with dispersal behaviour, whereas PC2 was primarily associated with inspection and feeding on a novel item (Table 2).

Correlations between behavioural variables differed within spring and river fish. Within spring fish, the only significant correlations were between non-independent variables derived from the same assays (Fig. 5a). These correlations,

for example between inspection and feeding latency, suggest that these variables are measuring the same behavioural trait within one assay and, therefore, are not indicative of behavioural syndromes. In contrast, within river fish significant correlations were found between multiple variables from the dispersal and novel environment assays (Fig. 5b), with more active river fish dispersing further and being more likely to disperse completely. Highly active river fish also used maze edges more and reached the maze endpoint more quickly. Similarly, river fish that reached the end of the maze faster also used maze edges more, dispersed further and were more likely to disperse completely.

Discussion

Divergence in desert goby personality

The desert goby shows complex intraspecific variability in behavioural traits that varies according to size, sex and habitat type. At the habitat level, intraspecific differences were observed in activity level, dispersal tendency and

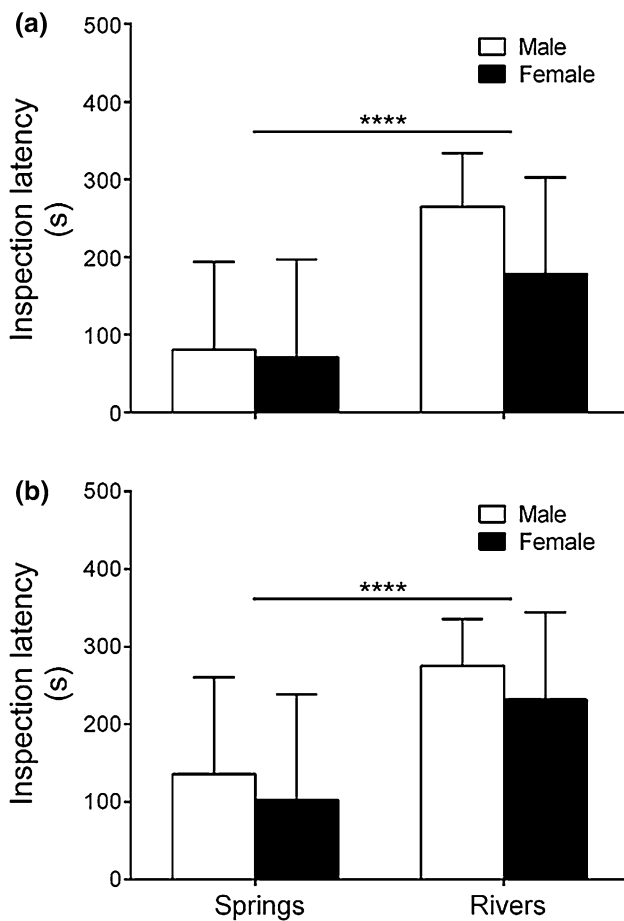


Fig. 3 Behavioural variability in novel item trials, including the effects of habitat type on an individual's **a** inspection latency and **b** feeding latency ($n = 67$). Error bars = 1 standard deviation

bold-exploratory traits. Although this study includes only two populations per habitat type, the results mirror previous research establishing habitat to be a primary driver of behavioural divergence in wild desert goby populations (Moran et al. 2016). Furthermore, we saw behavioural differences due to sex and length in activity and bold-exploratory traits within a novel environment. These results highlight the importance of considering body size and sex effects on intraspecific behavioural variability.

Divergence in bold-exploratory traits have been observed across multiple ecological scales in wild guppies (*Poecilia reticulata*), including between-population and between-sex differences (Harris et al. 2010). Another poeciliid fish, the Panamanian bishop (*Brachyrhaphis episcopi*), has been shown to differ in refuge emergence between populations and according to body size (Brown and Braithwaite 2004). Behavioural differences at these levels may be associated with variation in metabolic requirements, susceptibility to predation, or sex-based differences in breeding and courtship (Careau et al. 2008; Schuett et al. 2010). In contrast to Panamanian bishops, refuge emergence itself is not a significant axis of divergence in laboratory-reared desert gobies, but activity and edge use in a novel environment was a significant trait. Increased activity by female gobies within a novel environment may be due to the increased metabolic demands of breeding, and lower susceptibility to predation, as females have less distinctive mottled brown colouration compared to males' vibrant blue and yellow colouration (Wong and Svensson 2009). Nonetheless, our analysis suggests that the effect of habitat differences on these specific behaviours was the principle factor driving intraspecific behavioural divergence. Habitat type

Fig. 4 Rda analysis of repeatable behavioural variables. Behaviour vectors (grey) represent the component loadings of input variables. Population vectors (black) represent the mean PC1 and PC2 score from each population ($n = 64$)

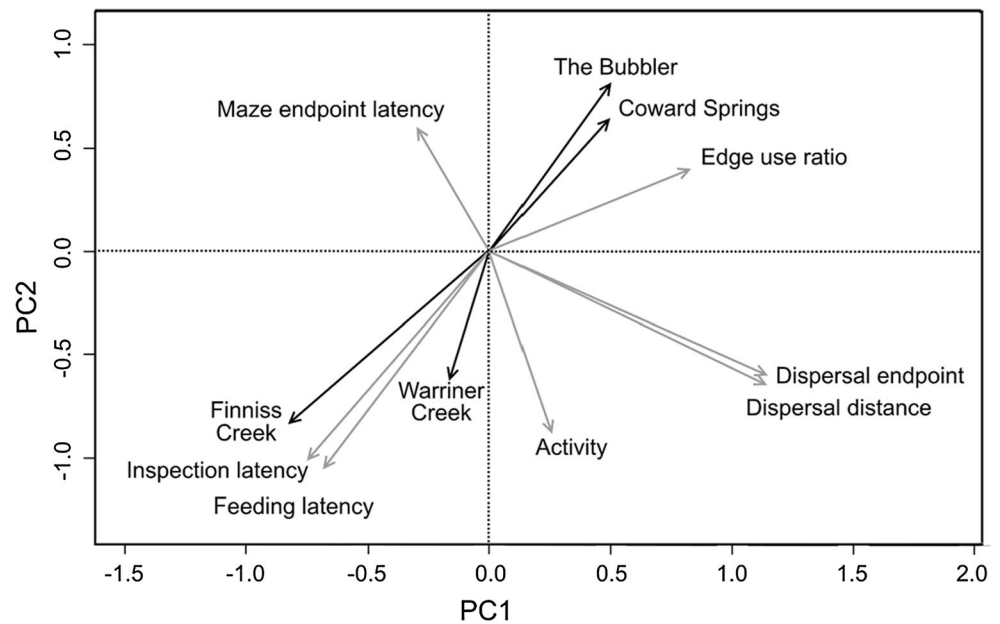


Table 2 Component loadings of PC1 and PC2 composite axes for all repeatable behavioural variables

Input variable	PC1	PC2
Activity	0.3266	-1.0836
Edge use	1.0362	0.4945
Maze endpoint latency	-0.3768	0.7473
Inspection latency	-0.9331	-1.2591
Feeding latency	-0.8464	-1.3102
Dispersal distance	1.4079	-0.7907
Dispersal endpoint	1.4133	-0.7411

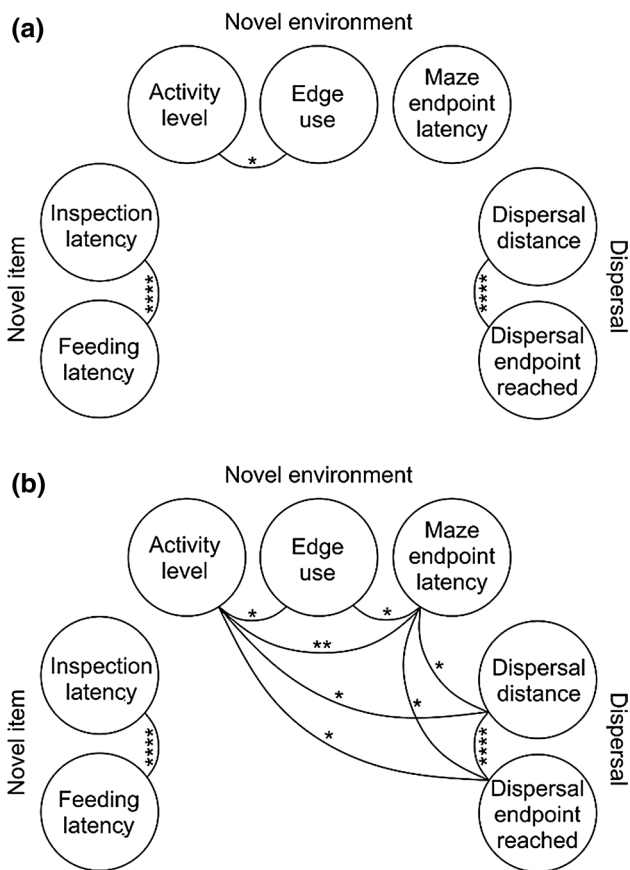


Fig. 5 Correlations between behavioural variables within **a** spring fish and **b** river fish. Lines represent significant correlations between variables (* $P < 0.05$, ** $P < 0.005$, **** $P < 0.0001$)

had significant effects on more behavioural variables, often with a larger effect size, and redundancy analysis including all variables found that habitat type was the only factor that had significant effects on the composite, PC1 and PC2, variables.

Habitat-based divergence between populations raised in a common garden show inherent behavioural differences between gobies that are likely to have a genetic, epigenetic and/or maternal basis (Buss and Greiling 1999; Herczeg et al. 2009; van Oers and Mueller 2010). Genetic

divergence may be the result of selective pressure, due to different ecological pressures from each habitat (Herczeg et al. 2009). Divergence may also be the result of spatial sorting of genotypes, particularly those related to dispersal traits, due to the differing spatial configuration of habitat types within their wider hydrological network (Lee 2011; Shine et al. 2011). Springs are often spatially distant from river channels, and, therefore, their populations can be isolated for extended periods of time, and relatively rare large-magnitude floods are required to provide dispersal corridors between spring and river populations (Kotwicki and Allan 1998; Wilmer et al. 2011). Genetic analysis of goby populations showed no evidence that our study region’s spring and river populations are isolated over evolutionary time (Mosop et al. 2015) and instead suggest that dispersal events are crucial to maintaining this surprisingly high genetic connectivity of aquatic habitat patches in a vast and dynamic desert landscape. Nonetheless, the behavioural divergence in novel environment and novel food item behaviours was not linked with dispersal traits in spring populations, suggesting spatial sorting of bold-exploratory traits is unlikely. Furthermore, selection can alter personality compositions over relatively rapid periods of time (O’Steen et al. 2002; Bell and Sih 2007; Adriaenssens and Johnsson 2013), so it is likely that selection due to contrasting ecological conditions between habitats is a major driver of the behavioural divergence observed between desert goby populations.

Habitat differences were associated with variation in multiple bold-exploratory traits. Spring gobies were faster to inspect and feed on a novel item, which is likely to be associated with differences in the ecological pressures faced by goby populations, such as the reduced predation pressure due to the lack of aquatic predators in springs. Predation has been shown to suppress boldness in populations of Eurasian perch (*Perca fluviatilis*) and enhance boldness in Panamanian bishop populations; the direction of the effect appears to depend on the relative fitness costs of risk-taking behaviour on susceptibility to predation and loss of foraging opportunities (Brown et al. 2007a; Magnhagen et al. 2012). Similarly, river fish used the edges of corridors in a novel environment more than spring fish, which may be associated with predator avoidance (Archard and Braithwaite 2011). When sampling wild river populations, we found that gobies tended to occupy shallow edge environments, potentially to avoid larger bodied aquatic predators, and this could be interpreted as a risk avoidance strategy. These responses further highlight the ecological and evolutionary significance of behaviours involving novelty, and a potential role of predation in the habitat-based divergence supports the proposition that novelty in nature involves intrinsic elements of risk-taking (Robertson et al. 2013). Furthermore, divergence in these traits between laboratory populations suggests that personality is associated with the fitness of gobies in these contrasting habitats.

High intraspecific competition can also influence behaviour (Amarasekare 2004; Dochtermann et al. 2012) and that spring populations likely experience intense space and resource competition is a potential explanation for habitat-related divergence. Decreased activity in spring fish reduces metabolic requirements, and increased neophilia may be a response to increased food competition (Careau et al. 2008). Disentangling competition and predator effects is troublesome because of their intrinsic non-independence (Chase et al. 2002). Network approaches to ecosystem analysis, such as food-web analysis, can potentially account for emergent and interactive effects of stressors (Layer et al. 2011) and may be valuable in understanding individual trait variability in a broader ecological context. Viewing intraspecific variability and animal personalities within a broader ecological context may also allow us to incorporate their potentially stabilising effects in population and food-web dynamics (Bolnick et al. 2011) and selection based on stability (Borrelli et al. 2015). This may be particularly relevant to understanding the ecological significance of risk-taking traits, which are closely related to food-web interactions like predation, competition and diet.

Divergence in syndrome structure

Personality is related to dispersal in river gobies: we saw that behaviour in a novel environment was correlated with dispersal tendency. Personality has been linked to dispersal in previous studies, specifically boldness in roach (*Rutilus rutilus*), a freshwater fish (Chapman et al. 2011), and sociability in mosquitofish (*Gambusia affinis*; Cote et al. 2010b). Our results show that there were consistent differences in dispersal tendency between gobies, and this was correlated with behaviour in a novel environment, but only in river fish. Specifically, river fish that were more dispersive were also quicker to reach the end of the maze, used the edges of the maze more and were more active. Conversely, behavioural responses to a novel item were unrelated to dispersal. This suggests that the habitat divergence in neophilia and activity is associated with the differing selective pressures of spring and river habitats and is unlikely to be the result of spatial sorting of behavioural phenotypes (Lee 2011; Shine et al. 2011). Notably, with syndrome analysis that uses multiple correlations between numerous variables, it can be appropriate to include a correction to account for the increased likelihood of type I errors (Dingemanse et al. 2007; Dochtermann 2010). This was not considered necessary due to the high number of correlations detected between dispersal and novel environment variables in river fish. This provided robust evidence that behaviour in these assays was not independent, without placing excessive weight on the significance of a single correlation. The correlations suggest that the behavioural syndromes in river gobies are adaptive responses to

ecological pressures in river habitats, specifically the need to disperse to persist across a largely ephemeral river network.

These correlated behaviours provide insights into the mechanisms that underpin behavioural syndromes in animal populations. Specifically, the difference between spring and river fish in behavioural correlations suggests that syndromes are not constraining the adaptive responses of gobies to different habitats (Sih et al. 2004). These results are consistent with the findings of studies that have shown divergence in correlated behaviours between populations of the same species (Dingemanse et al. 2007). This supports an adaptive hypothesis, i.e., that correlations should arise where selection favours covariance between traits and that these correlations can arise rapidly in populations over ecological timescales (Bell 2005; Dingemanse et al. 2007; Moya-Larano 2011). Our findings highlight the significance of intraspecific behavioural variability to the adaptive responses of animals to complex ecological pressures and that these responses are essential to the desert goby persisting in challenging desert environments.

Author contribution statement NPM, KDM and BMW conceived and designed the experiments. NPM performed the experiments and analysed the data. All authors contributed to the writing of the manuscript and by providing editorial advice.

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Compliance with ethical standards

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed. Approvals and permits were granted by the Monash University Animal Ethics Committee (BSCI/2012/14, BSCI/2012/22), the South Australian Department of Environment, Water and Natural Resources (Q26166-1, Q25886-3) and Primary Industries and Regions SA (ME 9902391, 9902523, 9902598 and 9902599).

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Conflict of interest The authors declare that they have no conflict of interest.

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