



Boldness in extreme environments: temperament divergence in a desert-dwelling fish



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Investigating how environmental factors influence within-species trait variability is critical to understanding the evolution and maintenance of individual behavioural differences (i.e. temperament or personality), and their integration into wider ecological theory. Populations of Australian desert gobies, *Chlamydogobius eremius*, from starkly contrasting aquatic environments in arid Australia were used to investigate how environmental differences influence temperament traits. Focusing on boldness and exploration, fish were assessed using novel environment, dispersal and novel food item assays under laboratory conditions. The results of these experiments were analysed for repeatability and for patterns of divergence within and between populations. We found consistent within-species differences in novel environment and novel food item assays, with refuge emergence and inspection latency of a novel food item both strongly repeatable behavioural axes. Although both traits can be considered measures of boldness, refuge emergence significantly diverged according to sex, while inspection latency was predicted by habitat differences. This suggests that multiple measures of boldness are diverging independently according to different ecological drivers. Specifically, we found that fish caught from environments without predators and with probable intense intraspecific competition are less active and bolder in a novel food item context. Further analysis demonstrated how extreme habitat differences are driving behavioural divergence on multiple axes, relating to boldness and dispersal behaviours. This provides valuable insights into how the environment and behaviour interact and how we define temperament traits, as well as highlighting the importance of studying temperament within a community ecology context.

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Animals persisting in any ecosystem face a complex suite of ecological challenges. For example, the ecological community to which an animal belongs can impose multidimensional pressures, including inter- and intraspecific predation and competition (Johnson & Stinchcombe, 2007). Behaviour is particularly important to an animal's adaptive responses to complex stressors (Dingemanse & Wolf, 2010). Animal temperament is a rapidly developing research area focusing on consistent intraspecific differences in behaviour, and ecologists are increasingly realizing its importance, particularly in the context of behavioural responses to variable or changing environments (Dingemanse, Kazem, Reale, & Wright, 2010; Wong & Candolin, 2015). This shift reflects a growing understanding that the dynamics of intraspecific trait

variation have broad implications for how ecosystems function generally, from the landscape and population dynamics of species, to invasion biology and community level dynamics (Bolnick et al., 2011; Moya-Laraño, 2011; Wolf & Weissing, 2012).

Temperament traits (which we here consider to be synonymous with animal personality; sensu Brydges, Colegrave, Heathcote, & Braithwaite, 2008) are consistent differences in behaviour between individuals of the same species, which are repeatable across time and/or contexts (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Wolf & Weissing, 2012). The recent surge in temperament research is, in part, driven by the relatively recent discovery that temperament traits, such as boldness or aggression, are present in a wide range of taxa (Gosling, 2001), some of which include spiders (Keiser & Pruitt, 2014), birds (David, Auclair, Giraldeau, & Cezilly, 2012), mammals (Dammhahn & Almeling, 2012), fish (Archard & Braithwaite, 2011) and molluscs (Pruitt, Stachowicz, & Sih, 2012). Given that animals with individual temperament are likely to be present in the vast majority of ecosystems, researchers are

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increasingly turning their attention to its ecological consequences (Wolf & Weissing, 2012). For example, ecological modelling suggests that temperament may influence the stability of biological communities, both as a source of intraspecific trait variability (Bolnick et al., 2011) and through its effects on an individual's or population's ability to adapt to environmental conditions (Sih et al., 2015; Valdovinos, Ramos-Jiliberto, Garay-Narváez, Urbani, & Dunne, 2010).

Exploring the relationship between temperament and environmental factors is crucial to understanding the role of inter-individual variability in driving community dynamics. Temperament traits can vary in consistency across time and contexts, and functionally different temperament traits can be correlated (i.e. in behavioural syndromes, such as a correlation between aggression and boldness; Sih, Cote, Evans, Fogarty, & Pruitt, 2012). The rigidity of personality types and behavioural syndromes may be potentially maladaptive by inhibiting the optimal behavioural response in a given ecological context. For example, bold animals may be consistently bold across contexts, including situations in which boldness has negative consequences (e.g. hatchery-reared fish are often highly bold leading to increased susceptibility to predation in the wild; Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011; Sih et al., 2012). None the less, empirical research shows that personality traits are both partially consistent and partially responsive to environmental conditions, which can assist responses to environmental pressures individually and at a population level (Dingemanse et al., 2010; Harris, Ramnarine, Smith, & Pettersson, 2010). For example, individuals can show plastic personality responses to various ecological pressures, including diet variability (Chapman, Morrell, & Krause, 2010), food resource competition (Dochtermann, Jenkins, Swartz, & Hargrett, 2012) and predator exposure (Bell & Sih, 2007).

Selection due to fitness differences between personality types can lead to rapid shifts in temperament at a population level. For example, Bell and Sih (2007) showed rapid shifts in the personality composition of a population of three-spined stickleback, *Gasterosteus aculeatus*, as a response to increased predation pressure. The population was more aggressive and less bold, as a result of both personality-biased selection and plastic personality changes in those individuals that survived predator exposure. The combination of consistency of behaviour (which can extend to heritability of personality types) and plastic personality responses is likely to be a reflection of the multiple mechanisms that can underpin variation in temperament, i.e. genetic, epigenetic and ontogenetic effects (Buss & Greiling, 1999; Koolhaas, de Boer, Buwalda, & van Reenen, 2007; van Oers & Mueller, 2010). So while there may be constraints on behavioural responses to ecological pressures (Conrad et al., 2011; Sih et al., 2012), behaviour may also be adapted to multiple pressures over various ecological scales (Moya-Laraño, 2011). Yet studies that directly measure patterns of intraspecific behavioural divergence and their relationship with environmental characteristics are still relatively rare, despite their importance to understanding population and community dynamics.

Recent empirical studies of animal temperament have revealed the complexity of intraspecific behavioural traits, particularly in terms of the range of axes of divergence. The major axes of temperament are boldness, sociability, activity, exploration and aggression, which may be used singularly or collectively to describe an individual animal's 'personality type' (Réale et al., 2007). However, the behaviours that constitute personality traits remain unresolved, and important contemporary research is now targeting quantification of temperament axes and relationships to ecological contexts. For example, boldness, which refers to an animal's tendency to undertake risky behaviours, can involve multiple classes of behaviour, including neophilia, predator response and

emergence into a novel environment (White, Meekan, McCormick, & Ferrari, 2013). These boldness behaviours can be correlated with each other, constituting a boldness syndrome (Brown, Jones, & Braithwaite, 2007). However, recent work has shown boldness traits can diverge independently. For example, Beckmann and Biro's (2013) study of damselfish, *Pomacentrus* spp., found that boldness as measured by refuge emergence was unrelated to boldness as measured by response to a fright stimulus. White et al. (2013) further found that only some boldness axes in damselfish had implications for their fitness. Réale et al. (2007) argued that the lack of clear definitions of temperament traits and limited understanding of the ecological contexts in which these traits are relevant are key barriers to integrating temperament into wider ecological theory. This demands further detailed studies of temperament traits, both laboratory and field based, that observe divergence patterns across multiple traits and ecological contexts.

The Australian desert goby, *Chlamydogobius eremius*, and the aquatic ecosystems in the Lake Eyre Basin of arid central Australia provide an exceptional opportunity to analyse patterns of temperament across an ecological gradient. This fish inhabits both the shallow groundwater springs fed by the Great Artesian Basin and the largely ephemeral desert rivers (Mossop et al., 2015). Both habitats have substantial biodiversity value and function as key refugia in the landscape, with springs being particularly important to the goby (Davis, Pavlova, Thompson, & Sunnucks, 2013). As Lake Eyre's rivers are among the most hydrographically variable rivers globally (Puckridge, Sheldon, Walker, & Boulton, 1998), these habitats can at times differ in abiotic conditions from springs. Abiotic conditions may have effects on trait development and also on an individual's ability to acclimate to new environments, including to laboratory conditions (Beaman, White, & Seebacher, 2016). None the less, gobies have extremely broad physical tolerances, suggesting that relatively minor abiotic differences are unlikely to drive trait variability (Thompson & Withers, 2002). Across these habitats, the desert goby is subject to contrasting ecological pressures. In the isolated and extremely hydrologically stable artesian springs, populations are likely to experience constant, high levels of intraspecific resource competition, due to their consistently high densities in physically small habitats free of aquatic predators. In rivers, goby populations are likely to experience greater predation pressure and interspecific competition due to the presence of other, often predatory, fish species (Michelangeli & Wong, 2014). As boldness traits have been shown to be related to environmental pressures such as predation (Herczeg, Gonda, & Merilä, 2009), competition (Dochtermann et al., 2012) and diet variability (Chapman et al., 2010), these water bodies offer an excellent opportunity to investigate how multiple boldness measures differ between individuals from contrasting ecological settings.

The necessity of dispersal to the persistence of desert gobies in a landscape of predominantly ephemeral water bodies allows us to explore the relationship between boldness and movement behaviours. Studies in other taxa have shown boldness personality traits to be related to exploration and dispersal behaviours: for example, bolder roach, *Rutilus rutilus*, in a refuge emergence assay had higher migratory propensity than shy individuals (Chapman et al., 2011). Furthermore, dispersal behaviours are particularly relevant in desert gobies considering the species' large range and occupancy of ephemeral habitats (Mossop et al., 2015). Boldness and movement behaviours are therefore likely to be important for understanding the landscape ecology of a species (Sih et al., 2012).

Accordingly, using the remarkable desert goby as a model, this study aimed to determine: (1) variation in temperament traits in a single species that spans habitats with highly divergent physical and community characteristics; (2) whether such traits are related

to environmental factors such as habitat type; (3) the relationships between various temperament axes; and (4) whether there is evidence that personality plays a role in the wider dispersal and landscape ecology of this species. Given this system's contrasting habitat types and ecological pressures, we anticipated that multiple behavioural traits would show divergence between populations, particularly in behaviours related to boldness, which may be the result of selective pressure, epigenetic or environmental effects. We expected that in habitats without aquatic predators and with high intraspecific competition, i.e. artesian springs, gobies may have increased boldness as an effective strategy to access food resources without the greater predation risk that is often associated with elevated boldness (Bell & Sih, 2007; Herczeg et al., 2009). Additionally, the role of artesian springs as permanent ecological refugia for the desert goby among a larger ephemeral river network (Davis et al., 2013) suggests that these populations may diverge in dispersal behaviour, where springs may be associated with a heightened dispersal tendency as a strategy to mitigate intense resource competition (Amarasekare, 2004). Furthermore, the goby's tendency to disperse may be correlated with certain temperament traits, such as in Chapman et al. (2011) where more dispersive fish were also bolder in a refuge emergence/novel environment context.

METHODS

Study Populations

Wild populations of desert gobies from the arid zone of northern South Australia were used for the study. Sites (Table 1) included three artesian springs, and three riverine waterholes, which ranged from permanent to semipermanent. Point water quality data (including temperature and conductivity) were collected annually in autumn (March–April) from 2013 to 2015, to characterize the abiotic characteristics of the sites (Hach HQ40d Meter, Hach 2100Q Turbidity Meter, Hach Pacific Pty Ltd, Notting Hill, VIC, Australia). Mean abiotic conditions during our study were similar between study sites and habitat types (excluding the very salty Warriner Creek), particularly relative to the broad abiotic tolerance range of gobies (Thompson & Withers, 2002). Fish were collected in autumn

2013 using a consistent approach to minimize potential personality-biased sampling (Michelangeli, Wong, & Chapple, 2015), which combined hand dip nets and box traps (30 × 20 cm and 20 cm high, 5 cm aperture, mesh size 1 mm, SureCatch, Singapore). Up to 50 fish per site were transported to Monash University according to previously published methods (Wong & Svensson, 2009) and housed in large stock aquaria (80–110 litres). The fish were maintained in controlled conditions (25 ± 1 °C, 12:12 h light:dark cycle) with consistent fish density and sex ratios (25–30 individuals per stock tank, 50:50 male:female ratio). Gobies are strongly sexually dimorphic, with male blue-yellow fin coloration being a key characteristic used to sex individuals (Wong & Svensson, 2009). A standard diet, to which all populations readily acclimate upon relocation to laboratory housing, was fed to the fish before and during the experimental period (Otohime EP 1 1.5 mm hirame pellet, Marubeni Nisshin Feed Co Ltd, Tokyo, Japan). As the salinity/conductivity of source habitats varied on collection, the fish were acclimated to a standardized conductivity over a 2-week period (7.0 ± 0.5 mS/cm).

Behavioural Experiments

On day 1, study fish ($N = 82$) were selected from stock tanks and placed into an individual 3-litre 'home tank' (10 × 25 cm and 20 cm high) within a recirculating housing system for individual identification (AHT3-2E 3-Shelf Benchtop, Aquatic Habitats, Cary, NC, U.S.A.). On days 2 and 3 of the experimental period, individuals were subjected to a novel environment and dispersal assay, in random order to eliminate bias associated with carryover effects (Bell, 2013). On day 10, fish were subjected to a novel food item assay. Unlike other assays, this was conducted after the other trials to allow the fish an extended acclimation period within their experimental tank. As this trial was conducted within the home tank, this extended acclimation was used to avoid conflating novel environment and novel food item behaviours, and to allow sufficient time to minimize carryover effects from the previous assays (Bell, 2013). All assays were conducted under the same physical conditions as the fish were housed in, with temperature and conductivity kept within a strict range (25 ± 1 °C, 7.0 ± 0.5 mS/cm). The fish were measured for size after completing the three assays, so

Table 1
IDs and habitat information for sites from which fish were collected

Site	ID	Latitude° / Longitude°	Habitat type	Conductivity (μS/cm)		Temperature (°C)		Notes on the fish community
				Mean	Range	Mean	Range	
The Bubbler	SPR1	−29.446483°/136.857849°	Artesian groundwater spring	5746	5490–6127	29.7	29.1–30.5	The desert goby is the only fish species present
Coward Springs	SPR2	−29.400388°/136.794193°	Artesian groundwater spring	6769	6550–6980	24.3	22.2–26.9	The desert goby is the only fish species present
Blanche Cup	SPR3	−29.452850°/136.858733°	Artesian groundwater spring	7100	6809–7270	20.9	20.2–21.7	The desert goby is the only fish species present
Algebuckina	RIV1	−27.899995°/135.814456°	Permanent river waterhole (Neales catchment)	8200	2900–12 150	23.9	12.9–32.3	Nine species present, including aquatic predators the golden perch, <i>Macquaria ambigua</i> , spangled perch, <i>Leiopotherapon unicolor</i> , and barred grunter, <i>Amniataba percoidea</i>
Warriner Creek	RIV2	−29.137986°/136.568422°	Ephemeral river waterhole (Warriner catchment)	57 268	35 400–78 704	20.7	19.2–22.1	Lake Eyre hardyhead, <i>Craterocephalus eyresii</i> , also present. Likely to include additional species, although fish surveys have not been undertaken
Finniss Creek	RIV3	−29.610250°/137.458289°	Permanent river waterhole (Finniss catchment) with groundwater spring inputs	12 900	12 690–13 030	23.0	18.6–26.9	<i>C. eyresii</i> and <i>L. unicolor</i> also present. May include additional species, although fish surveys have not been undertaken

that potential age or life history effects on behaviour could be accounted for, by placing the individual in a clear container overlaying a 1×1 cm reference grid and taking an aerial photograph from approximately 20 cm above the fish. Total length (i.e. head to tail fin tip) was measured later using image processing software (ImageJ 1.50b, National Institutes of Health, Bethesda, MD, U.S.A.).

Novel environment assay

The willingness of a fish to emerge into a novel environment has been shown to be associated with boldness (Brown, Jones et al., 2007), and the 'standard refuge emergence protocol' or 'open field paradigm' has become a common measure of boldness in many species (Dingemans, Both, van Noordwijk, Rutten, & Drent, 2003), including fish (Chapman et al., 2011). The novel environment (Fig. 1a) was a maze similar to that used in Chapman et al. (2010). The focal fish was placed in an enclosed refuge (15×15 cm and 15 cm high) within a novel environment. After a 15 min acclimation period, a door (7.5×4 cm) was opened remotely, and the time taken for the fish to completely emerge from the refuge into the novel environment was recorded. Latency was set at 15 min so that fish that did not emerge in that time ($N = 4$) were given the maximum score (900 s), similar to the approach of Chapman et al. (2011) and Brown and Irving (2014).

The focal fish was then given 10 min from the time of emergence to explore the novel environment (Fig. 1a). Between trials the arena was completely drained, rinsed with reverse osmosis (RO) water and the water replaced, to limit the presence of odours or chemical cues left by previous fish that may influence behaviour in subsequent trials. To eliminate the possibility of disturbance to the fish caused by the presence of the human observer, trials were scored remotely (i.e. from a separate room) via two aerial CCTV cameras

positioned 1 m above the maze. A range of variables were recorded to characterize behaviour in the novel environment, including activity level (i.e. grid squares entered/s), area of maze explored (i.e. number of grid squares explored), length of maze explored (i.e. number of nine-square segments explored), use of maze edges (i.e. ratio of edge:nonedge squares explored). A fish was considered to have entered and explored a square if >50% of the fish's body was within the grid square.

Dispersal assay

A larger scale dispersal assay was included to further investigate the role of boldness and exploratory behaviours in this species, as recent work has established links between personality traits and dispersal in other fish taxa (Chapman et al., 2011). A laboratory assay approach was used to test dispersal tendencies in individuals, modelled off similar experiments in other fish species (Rehage & Sih, 2004). The apparatus used a cascading series of pools, representing habitat patches, connected by riffle channels (1 m long with a minimum depth of 2 cm), which only allowed one-way dispersal between pools. These mimicked a typical habitat structure encountered by gobies in the wild, i.e. shallow interconnected pools, and therefore provided a relevant test of dispersal tendency for all populations. The four pools (127×84 cm) were filled to approximately 15 cm with aged filtered tap water (25 ± 1 °C, 7.0 ± 0.5 mS/cm) and included a layer of 2 mm gravel, six identical plastic aquarium plants and six halved ceramic pots for refuge. An inline pump (Heto Brand, Hengtong Aquarium Co. Ltd, Guangdong, China) connecting the bottom to the top pool created a recirculating system with a flow averaging 370.4 ml/s. An extended 40 min acclimation in the top pool allowed the focal fish sufficient time to acclimate to the flow rate, and reduced the likelihood of accidental dispersal events. Following this, a barrier preventing dispersal was removed from channel 1 and fish were allowed 3 h to disperse. A digital video recording system (DVR4-2000, Swann Communications Pty Ltd, Port Melbourne, VIC, Australia) was used to film the channels, to record the exact time of dispersal events. Dispersal distance (i.e. number of pools), latency to the first dispersal event and latency to reach the final pool were each scored.

Novel food assay

On day 10, fish were subjected to a novel food assay (Fig. 1b). Assessing an animal's willingness to inspect a novel item, as well as feed on novel foods, is a common approach to quantifying bold or shy temperaments within individuals (Dingemans et al., 2007). To achieve this, focal fish were presented with a novel food item placed within their individual home tank (10×25 cm). Specifically, a 0.1 g cube of lamb liver was dropped manually with 25 cm forceps. During the trial, opaque partitions were placed on each side of the tank so that the fish was unable to see the observer dropping the item into the tank. Partitions were put in place 30 min before the trial was initiated. Liver was chosen as a food item that this species would not have experienced in natural ecosystems or in the laboratory. Additionally, liver has been used to feed experimental fish (Adriaenssens & Johnsson, 2013) and pilot trials using separate, nonexperimental individuals showed that a significant proportion of desert gobies were willing to attempt to feed on this item within a short (<5 min) time frame. The fish were given 5 min to inspect and attempt to feed on the novel food item. Trials were filmed (Canon Powershot S100 Digital Camera) beginning 5 min before trial initiation, to minimize observer effects from turning on the camera. Inspection latency (i.e. time until the fish actively swam to within 2.5 cm of the novel item) and feeding latency (i.e. time until the fish attempted to feed on the item) were scored.

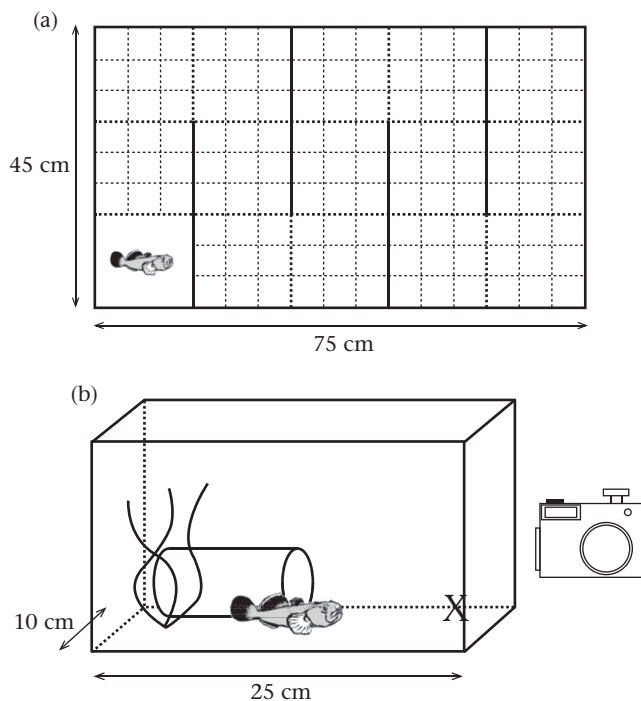


Figure 1. (a) Novel environment assay, aerial view, and (b) novel food assay, lateral view. The novel environment is a 75×45 cm tank divided into corridors filled to a 10 cm depth. External walls are opaque white, and internal walls are 30×15 cm acrylic white sheets. The area is divided at two scales shown by the dashed lines: 14 major (15×15 cm) and 126 minor (5×5 cm) grid squares. The novel food item (marked X) is dropped in the front end of the tank where a camera is set up to record behaviour during the trial.

Ethical Note

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 South Australia (ME 9902391, 9902523, 9902598 and 9902599). All research was conducted in accordance with approved guidelines and methods. All trials were noninvasive and acclimation periods were used to minimize stress associated with moving individuals between tanks and assays, thereby reducing any adverse effects on the welfare of animals as much as possible. Following their use in this study, animals were retained for use in other, unrelated research.

Statistical Analysis

All statistical analyses were conducted using R Statistical Package 3.1.2 (R Core Team, 2014). To establish which variables showed repeatable differences between individuals, and therefore constitute meaningful measures of intraspecific behavioural divergence in this species, a subset of 35 individuals (approximately six per population) were randomly selected from the experimental population to be run through each assay twice (Herde & Eccard, 2013). This was done 4–6 weeks after their initial trials to test repeatability over a wide temporal context. Repeatability was assessed using Spearman rank correlations between the first and second trial scores for each variable, giving a nonparametric measure of each variable's consistency across all 35 individuals (Brown & Irving, 2014; Herde & Eccard, 2013). To further characterize trait consistency, the intraclass correlation coefficient of each variable was calculated (ICC package; Wolak, Fairbairn, & Paulsen, 2012). To focus subsequent analysis on divergence in variables that can be characterized as consistent phenotypic differences in behaviour, i.e.

temperament traits, only significantly repeatable variables were included in statistical analysis of behavioural differences associated with habitat, sex and body length.

Variables were checked for normality (using the Shapiro–Wilk test) and transformed where necessary (Table 2). Normally distributed variables (emergence latency, activity and edge use) were analysed using an 'lmer' general linear model (lme4 package; Bates, Maechler, Bolker, & Walker, 2015) using habitat type and sex as predictor variables nested within population, as well as total length of fish as a continuous covariate. Sex and length were included to account for these potential sources of behavioural variability within populations (Harris et al., 2010). Tukey contrasts were used to test the significance of habitat and sex effects on variables. A similar approach was used for inspection latency, instead employing generalized linear mixed-effects models (GLMM) due to the truncated assay time producing a heavily bimodal distribution (Bolker et al., 2009). A binomial data set was produced for inspection latency by partitioning the data into 1 (latency < median score) or 0 (latency > median score), similar to the approach of Brown, Jones et al. (2007). The median score of the data set was 132.5 s, where individuals that inspected the item before this time were characterized as rapid inspectors.

Relationships between all repeatable variables (i.e. activity and edge use) were investigated with Pearson correlations, using all available data points. In addition to this, untransformed data was entered into a redundancy analysis (RDA; vegan package; Oksanen et al., 2015) to investigate the relationship between behaviours across the three assays. This was specifically used to test whether behaviours in each of the three assays were independent, whether divergence between populations was multidimensional and how variables associated with boldness traits related to dispersal behaviour. As several individuals did not emerge into the novel environment and activity and edge use scores were unavailable, this analysis was conducted using emergence latency, inspection

Table 2
Definitions and repeatability estimates for key behavioural variables

Variable	Assay	Normality	Spearman's rho	Intraclass correlation coefficient, ICC (95% CI)	Description
Emergence latency	Novel environment	Normalized with $\ln(1+x)$ transformation	0.406 ($P=0.016$)	0.335 (0.010, 0.597)	Time taken for fish to emerge from the refuge after a 15 min acclimation period. A fish was considered to have emerged once >2/3 of its body was outside of the refuge. Maximum latency was set at 900 s
Activity	Novel environment	Normal	0.396 ($P=0.023$)	0.187 (−0.163, 0.489)	The 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 it body was within the square
Edge use	Novel environment	Normalized with \ln transformation	0.360 ($P=0.040$)	0.328 (−0.009, 0.599)	To 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
Inspection latency	Novel food	Bimodal, converted to binomial for GLMM	0.488 ($P=0.003$)	0.447 (0.141, 0.676)	Time 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
Dispersal distance	Dispersal	Bimodal	0.269 ($P=0.119$)	0.267 (−0.065, 0.547)	The number of dispersal events between pools in a 3 h trial period, from 0 (no dispersal events) to 3 (complete dispersal into the final pool)

latency and dispersal distance. This allowed all data points (individual fish) to be included. For ease of interpretation, both inspection latency and emergence latency were negated, so that 'Bold (inspection latency)' and 'Bold (emergence latency)' vectors were positively related to higher boldness, which otherwise had no effect on subsequent analyses. Habitat differences associated with the PC1 and PC2 variables were analysed using linear models.

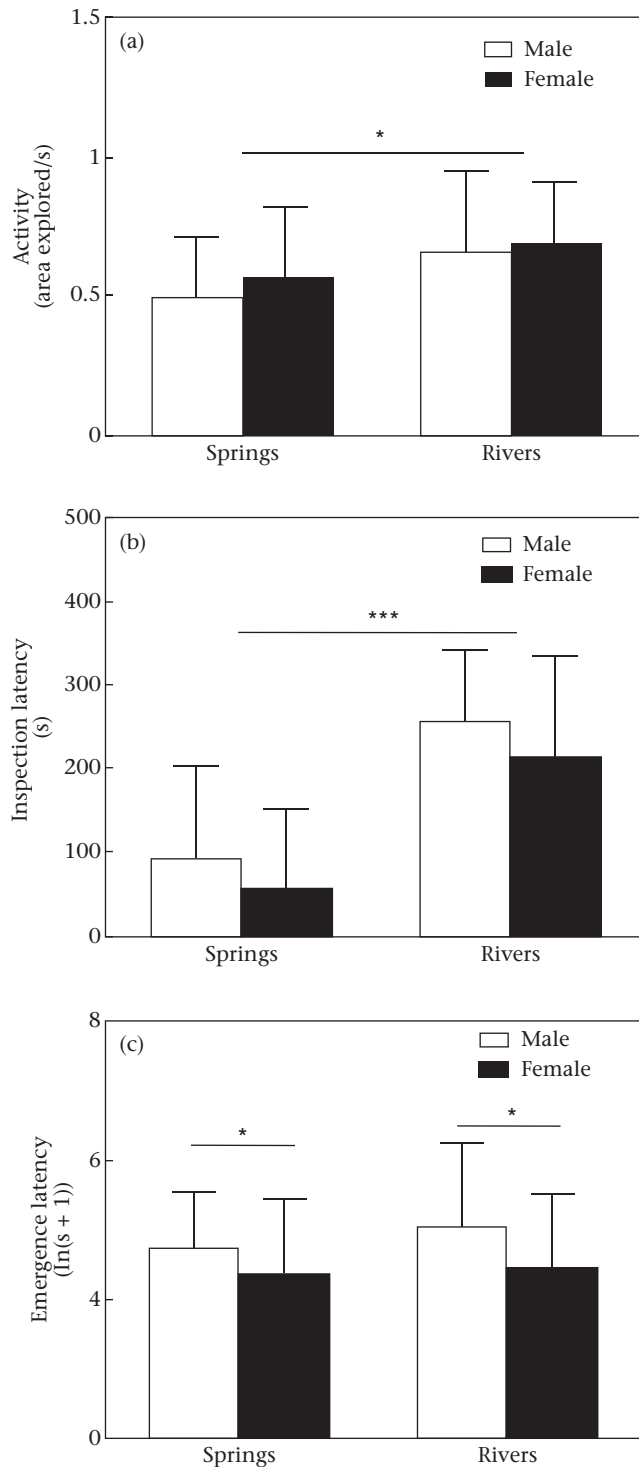


Figure 2. Habitat-based divergence in (a) activity in a novel environment and (b) inspection of a novel food item: * $P < 0.05$; *** $P < 0.0001$. (c) Sex divergence in emergence latency in a novel environment: * $P < 0.05$. Error bars indicate 1 standard deviation from the mean.

RESULTS

Temperament Traits in the Desert Goby

Repeatability, demonstrating consistent differences between desert gobies in behavioural responses within these assays, was significant in four variables (Table 2). ICC estimates are similar to population-adjusted ICC estimates (e.g. edge use $ICC_{adj} = 0.314$, emergence latency $ICC_{adj} = 0.279$; see method in Nakagawa & Schielzeth, 2010), although differences in estimates suggest the effects of population origin on repeatability requires further investigation. No significant repeatability was detected in variables from the dispersal assay, including dispersal distance (Table 2), and a majority of fish (50–60%) showed no dispersal behaviour in either dispersal trial.

Patterns in Trait Divergence

The sex and habitat type of fish populations significantly influenced several behavioural variables. Both activity level and inspection latency differed by habitat. Specifically, spring fish were less active ($Z = -2.29$, $P = 0.022$; Fig. 2a) and quicker to inspect the novel food ($Z = 4.204$, $P < 0.0001$; Fig. 2b) than river fish. Emergence latency showed no effect of habitat type, but an overall effect of sex, with females being quicker to emerge into a novel environment than males ($Z = 1.987$, $P = 0.047$; Fig. 2a). Fish length had no significant effects on these variables. Habitat, sex and fish length did not influence edge use.

Correlations Between Behavioural Axes

Inspection latency of a novel food item and edge use within the novel environment were correlated (coefficient = -0.339 , $N = 70$, $P = 0.046$), i.e. fish that were slower to inspect the novel item used the edges of the maze more in the novel environment. Within the novel environment assay, activity was correlated with both emergence latency (coefficient = -0.440 , $N = 78$, $P < 0.001$) and edge use (coefficient = 0.241 , $N = 77$, $P = 0.046$), suggesting these variables may potentially be nonindependent as they were scored simultaneously. There were no other significant correlations between repeatable behavioural axes or with dispersal distance.

Redundancy analysis found no significant relationships between inspection latency, emergence latency and dispersal distance (Fig. 3). However, the resulting combined axes, PC1 and PC2 (eigen values = 1.203, 1.117 respectively), explained a considerable amount (77.34%) of the variability in the three input variables. PC1 was closely related to dispersal (loadings: dispersal distance = 0.997, inspection latency = 0.460, emergence latency = -0.620), whereas PC2 was more closely aligned with boldness variables (loadings: dispersal distance = 0.075, inspection latency = 0.888, emergence latency = 0.785). Linear models showed that spring individuals were significantly different from river individuals on PC1 ($F_{1,72} = 5.389$, $P = 0.023$) and PC2 ($F_{1,72} = 36.67$, $P < 0.0001$), suggesting at least two distinct axes of behavioural divergence across the three behavioural assays (Fig. 3).

DISCUSSION

Desert gobies showed consistent within-species differences in behaviour on multiple axes, including the activity and boldness traits commonly used in temperament studies. Dispersal axes did not show consistent differences, although a larger number of individuals or trials may be required to detect this. Conversely, both emergence latency and inspection latency are significant axes of intraspecific behavioural variation in the desert goby, underscoring

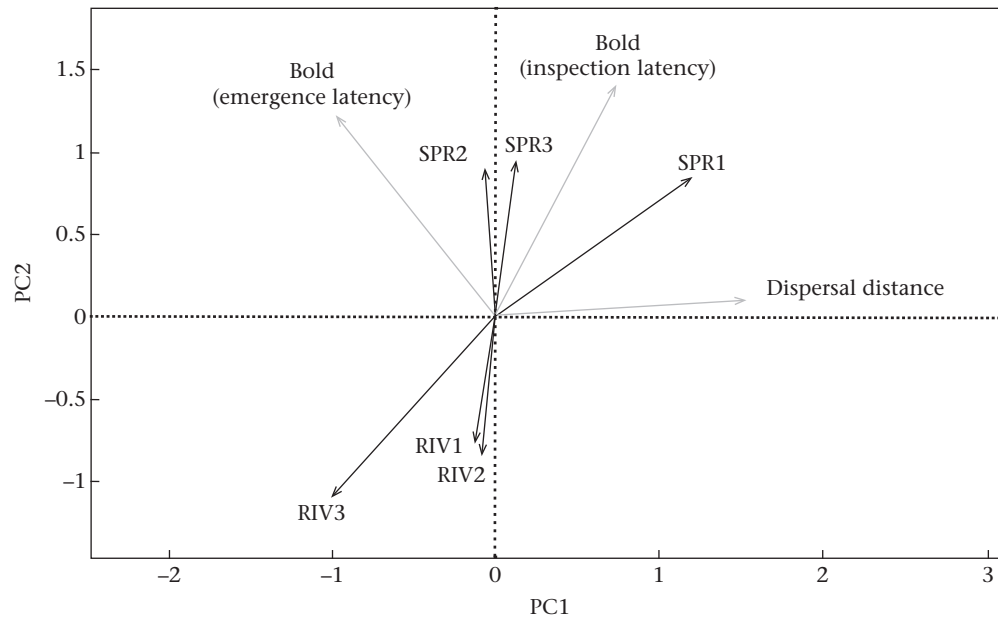


Figure 3. Redundancy analysis (RDA) of inspection latency, emergence latency and dispersal distance. Bold (inspection latency) and Bold (emergence latency) vectors are positively related to higher boldness. Population vectors represent the mean PC1 and PC2 score from each population.

that boldness traits are likely to have important effects on the ecological interactions of this species (Bolnick et al., 2011). As we used a laboratory assay approach to analyse temperament, an inherent limitation is the potential for induced captivity to alter the behavioural responses of fish. None the less, the distinct divergence patterns in these variables demonstrate consistent behavioural variation within and between populations (Figs. 2b,c and 3), which is relevant to how temperament traits are defined. Meaningful definitions of temperament axes are required to incorporate individual behaviour into ecological theory (Réale et al., 2007).

The sex-based divergence in emergence latency and habitat-based divergence in inspection latency in this study suggest that these boldness traits are relevant in different ecological contexts and are diverging independently. Divergence in inspection latency suggests that an ecological pressure associated with habitat type is influencing this trait, for example by selective pressure or plastic responses associated with greater predator exposure in rivers. Contrastingly, the sex difference in emergence latency appears in both springs and rivers, suggesting variance in this trait is unrelated to habitat-linked ecological pressures. Boldness is broadly defined as an individual's risk-taking tendencies, but incorporates multiple behavioural axes (Wilson, Clark, Coleman, & Dearstyne, 1994). These include neophilia (an animal's response to a new object both in food and nonfood contexts; Dingemans et al., 2007), willingness to enter and explore a novel environment (Chapman et al., 2011), responses to a predator (Chapman et al., 2010), and the willingness to forage and feed in risky areas (Dammhahn & Almeling, 2012). While these axes are often found to be correlated with each other (Brown, Jones et al., 2007), constituting a boldness syndrome, other studies have shown that different measures of boldness can diverge independently with differing ecological significance (Beckmann & Biro, 2013; White et al., 2013).

The differing effects of habitat and sex on the temperament traits in the desert goby suggest that current approaches to defining these traits are not entirely appropriate here and remain unsettled. Réale et al. (2007) argues that behaviour in contexts that involve novelty, such as emergence into a novel environment or inspection of a novel item, may be better characterized as exploratory

behaviour. This definition distinguishes exploration from boldness, where the latter should be primarily concerned with risky, but not novel situations such as predator response or risk-sensitive foraging. This diverges from the broader definition of boldness as an animal's tendency to engage in risky behaviour (Wilson et al., 1994). Responses to novelty involve inherent risks (Robertson, Rehage, & Sih, 2013), both in a novel object/food context, e.g. ingesting unsuitable or dangerous objects, and in a spatial context in exploring novel environments, e.g. moving to unsuitable/dangerous habitat patches. This component of risk is the basis for novelty responses to be considered boldness using the approach of Wilson et al. (1994). Whether emergence latency and inspection latency are considered exploration or boldness, their independent divergence in the desert goby suggests grouping them together in either category is inappropriate, and demonstrates that the frameworks used to define animal temperament traits remain unresolved.

There is little evidence suggesting that temperament is a constraint on the goby's ability to adapt to complex ecological pressures. The constraint hypothesis suggests that mechanisms that may underpin multiple temperament traits, e.g. hormonal or pleiotropic gene processes, may constrain adaptive responses to ecological pressures (Sih et al., 2012). Instead, the independent patterns of divergence across multiple axes of temperament seen in gobies, such as inspection latency and emergence latency, are arguably more in line with an 'adaptive' hypothesis. This proposes that behavioural syndromes may result from the combined effects of multiple ecological stressors on behaviour (Dingemans et al., 2007). The validation of this hypothesis would demonstrate the ability of temperament to be adapted to multiple ecological stressors operating at different scales (Moya-Laraño, 2011). This implies that temperament axes should be defined according to the ecological contexts to which they are relevant. For predator response boldness this context is self-evident, whereas for emergence/exploratory boldness this may include multiple contexts including foraging (Michelena, Jeanson, Deneubourg, & Sibbald, 2010) or mate-finding and nesting behaviour (Schuett, Tregenza, & Dall, 2010). By not unnecessarily conflating traits and instead

using ecologically relevant definitions, we may be able to understand how environmental factors shape personality and syndromes within animals.

The results of the current study show that habitat is influencing goby behaviour on at least two axes (Fig. 3), suggesting that the ecological characteristics of the habitat types are either directly or indirectly driving behavioural divergence. Differences in the local community composition, particularly the lack of aquatic predators in artesian springs, may potentially be influencing the boldness of goby populations. The effects of predation on boldness behaviour are relatively well documented experimentally (e.g. three-spined sticklebacks; Bell & Sih, 2007) and in the wild (e.g. crickets, *Gryllus texensis*; Adamo, Kovalko, & Mosher, 2013). Elevated predation commonly leads to reduced boldness, although the direction of response can vary depending on other factors, such as the relative fitness costs that reduced boldness may have in relation to foraging (Brown, Burgess, & Braithwaite, 2007). Boldness influences the outcome of predator–prey interactions (Pruitt et al., 2012) and both selection and plastic responses to predator exposure are mechanisms through which predator–prey interactions can influence temperament (Bell & Sih, 2007). Goby populations in the three riverine sites would be exposed to predation from larger fish when the river systems intermittently connect. At the time of sampling, only RIV1 and RIV3 contained large-bodied predators (e.g. *Leiopotherapon unicolor*), suggesting recent plastic or learned responses to aquatic predators are unlikely to be the cause of this behavioural difference in all three populations.

Although predation may be playing an important role in desert goby divergence, it is necessary to consider the combined effects of multiple interactions (i.e. predation, competition and feeding) on temperament to further understand how an individual's behaviour interacts with its environment. For example, spring populations lack large fish predators, but within the isolated and space-limited nature of the springs, competition for territory or resources is likely to be intense. As competition can influence personality (Dochtermann et al., 2012), elevated dispersal tendency in artesian spring individuals (Fig. 3) may be evidence of increased competition in spring populations (Amarasekare, 2004).

Disentangling the effects of multiple types of interactions on behaviour is problematic as effects may be confounded and non-independent. Herczeg et al. (2009) found that nine-spined sticklebacks, *Pungitius pungitius*, from isolated, predator-free ponds were more aggressive and bolder than marine populations, but differences in competition intensity and habitat structure meant that these differences could not directly be attributed to predation. Reduced predation pressure can increase inter- and intraspecific competition in prey species, illustrating the complex and non-independent nature of these responses (Chase et al., 2002).

The behavioural correlations in goby behaviour suggest that there may be a relationship between foraging, predation and temperament in the desert goby. Specifically, we found a correlation between inspection latency, which may be associated with foraging behaviour (Patrick & Weimerskirch, 2014), and edge use, which may be associated with predator avoidance (Archard & Braithwaite, 2011). This correlation may be a result of an ecological pressure that differs between sites, i.e. predation, concurrently affecting distinct traits by selection or plastic behavioural responses (Bell & Sih, 2007). Further analysis of laboratory-reared populations is being used to assess whether the behavioural variance observed in this study is associated with genetic or environmental effects, and specifically whether these behavioural correlations are simply the result of differing ecological pressures on each population. A common response to high predation pressure is reduced boldness (Magnhagen, Hellström, Borcharding, & Heynen, 2012), but the opposite response is arguably appropriate in situations in which the

negative fitness consequences of reduced boldness, for example lost foraging opportunities, outweigh the positive fitness effects of avoiding predation (Brown, Burgess, et al., 2007). The link between inspection latency and edge use suggests a trade-off between foraging opportunities and predation, such as that seen in the agama, *Agama aculeata*, in which bolder individuals bask and forage more but are subject to greater predation pressure than shy individuals (Carter, Goldizen, & Tromp, 2010). This demonstrates how ecological interactions influence animal temperament but their combined effects are likely to be nonindependent. An intriguing topic for future study may be disentangling these effects by assessing temperament responses to experimentally manipulated changes in both predation pressure and resource competition.

It is now becoming increasingly apparent that intraspecific trait variation, particularly temperament, has implications for how individuals and populations interact with their environment (Bolnick et al., 2011; Wolf & Weissing, 2012). Although multiple trophic interactions influence temperament, their combined and interactive effects are unresolved and a framework for analysing behaviour within a community context is lacking. Exploring the effects of multidimensional ecological pressures on behaviour requires further empirical studies of temperament across divergent communities as well as experimental investigation of the effects of multiple interactions on the development of animal temperament.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.09.024>.

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