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RESEARCH PAPER

The Association Between Personality Traits, Morphological Traits and Alternative Mating Behaviour in Male Endler's Guppies, *Poecilia wingei*

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Abstract

Alternative mating behaviour, personality traits and morphological characters are predicted to be correlated. Bolder, larger and more colourful males are expected to preferentially court females, while shy, small and drab-coloured individuals are predicted to sneak copulations. We used males of Endler's guppy, *Poecilia wingei*, to test this association over a long temporal period (hence including ontogenetic changes) and under two social environments (male-biased and female-biased). We found that personality traits (exploration, boldness, activity) of *P. wingei* males were highly repeatable across long time spans, but they were not correlated (formed no behavioural syndrome). Male age and social environment had no effect on any personality trait, despite their effects on alternative mating behaviour. Young males with higher activity levels were more likely to attempt sneaking. In older fish, there was an association between orange coloration, courtship and boldness, but this was not observed in young males. Our results suggest that alternative mating behaviour is more flexible than personality traits and is independent of them. Non-colour-based morphological traits (gonopodium length, body length, caudal straps length, dorsal fin length) were not correlated with any particular mating behaviour.

Introduction

Alternative mating behaviour (AMB) describes intrasexual differences in mating behaviour among individuals within a population to maximize their reproductive success. AMB is primarily performed by individuals with different competitive abilities and forms an important aspect of intrasexual competition for fertilization success (Oliveira et al. 2008). AMB can be fixed for life (Shuster & Wade 1991) but often is highly flexible (Candolin 2004), and its expression and success are affected by a range of environmental and demographic factors (reviewed in Kokko & Rankin 2006; Taborsky 1994).

The role of morphological traits (e.g. size and colour) on the adoption of AMB is well established (Andersson 1994). In contrast, more abstract sources of interindividual variation related to AMB, such as cognitive and personality traits, remain relatively neglected (Sih 2013; but see Smith et al. 2015), despite their potential to affect expression and success of the AMB. While it was demonstrated that different behavioural types had different reproductive (e.g. Dingemanse et al. 2005) and mating success (e.g. Reaney & Backwell 2007), our understanding of the links between personality traits and sexual selection remains surprisingly limited (Schuett et al. 2010; but see Godin & Dugatkin 1996; Schuett et al. 2011).

Personality traits possess a degree of plasticity (Galhardo et al. 2012; Thomson et al. 2012), and individuals can adjust their behaviour on the basis of external cues while still consistently differing from each other (Mathot et al. 2012). Social learning (Frost et al. 2007) and social experience (Modlmeier et al. 2014) should enable males to modulate their reproductive behaviour according to female responses.

Hence, males frequently rejected by females may benefit from adjusting their behaviour to support successful sneaking, while males receiving female interest may benefit from a different experience-based modulation of their behaviour. Personalities constrain the overall magnitude of these changes, but plasticity of their expression enables to modulate particular behaviours over time in relation to current individual condition and social environment (Piyapong et al. 2010; Thomson et al. 2012). Hence, there is scope for adaptive exploitation of variable social environment by males through modulation of personality-related behaviours (Bergmüller & Taborsky 2010).

We investigated a potential link between individual personality traits and AMB in the sneaker/courter complex and its response to contrasting social environments using Endler's guppy, *Poecilia wingei*, a small poeciliid fish. It is a sister species of the common guppy (*Poecilia reticulata*), with a largely similar suite of reproductive behaviours. Male *P. wingei* either court females using sigmoid displays and solicit cooperative mating or try to circumvent female choice by sneak (coercive) copulations. In *P. reticulata*, AMB is affected by diverse demographic and environmental factors (Houde 1997). Individual males vary greatly in their use of courting and sneaking and differ in the frequency of their switching (Houde 1997), implying that the use of AMB is flexible (Magurran & Magellan 2007). There is clear and repeatable interindividual variation in particular personality traits in *P. reticulata* (e.g. Budaev 1997; Brown & Irving 2014). As with many other taxa, guppy personality traits may be grouped into correlated suites of behaviours called behavioural syndromes (BSs) (Smith & Blumstein 2012). Personality traits also have considerable consequences for guppy individual fitness (Smith & Blumstein 2010) and, in another poeciliid fish, *Gambusia holbrooki*, personality can be modulated by a modification of environmental factors (Sinclair et al. 2014).

How social conditions affect expression of personality traits is less clear (but see Piyapong et al. 2010). Male *P. wingei* are capable of modifying their reproductive behaviour according to their phenotypic traits, social environment and intensity of sexual selection (Řežucha & Reichard 2014, 2015). It is not known whether there is any link between personality and AMB and, if so, whether personality traits and the use of AMB can be modulated. In this study, we tested the following: (1) the existence of personalities by testing repeatability of the main behavioural traits (exploration, boldness towards predator and general activity level) in *P. wingei* males and their possible formation into a BS; (2) the link between personality traits (particularly boldness, as indicated by predator inspection) and AMB, accounting for individual morphological traits; and (3) consistent changes in individual personality traits after 5 wk of exposure to contrasting social environments (female-biased × male-biased environment).

We predicted differences in personality traits and formation of distinct BSs between sneakers and courters. We expected that more conspicuous individuals (i.e. with more carotenoid coloration) would have a greater propensity towards predator inspection and would court females rather than sneak (Godin & Dugatkin 1996; Jirotkul 2000; Kiritome et al. 2012). Sneakers, being generally less colourful and thus less able to attract females (Houde 1997; Oliveira et al. 2008), were predicted to be more active in order to increase female encounter rate. Males from a female-biased environment (with no male rivals) were predicted to be bolder, but less active and explorative due to their unrestricted access to females and the lack of competition with rivals.

Material and Methods

Experimental Animals

Experimental fish came from our breeding stock composed of outbred descendants of *P. wingei* imported from Laguna de los Patos (northern Venezuela) in 2007. Over a period of 1 mo, all emerging juveniles were collected from the stock aquarium (120 l) and isolated in a separate 72-l aquarium. Juveniles were frequently sexed, and females were removed and kept separately.

Sixty-five males (approximately 18.5 wk old, sexually mature) were collected from the 72-l male stock aquarium and individually housed in 2-l plastic aquaria enriched with artificial plants. The aquaria were visually separated from each other. Fish experienced a natural light regime, and additional light was provided for 12 h a day (08:00–20:00) by a 40-W Sun Glo daylight spectrum fluorescent tube. Water temperature fluctuated between 22 and 25°C. Males were fed daily, and water was partly exchanged every 2 wk (for full details, see Řežucha & Reichard 2015).

Behaviour Trials Treatments

Behavioural trials were conducted in the same order for all subjects before and after change in the social environment, as recommended by Bell (2013). An alternative is to randomize the order of trials for each subject to minimize any potential 'carry-over effects'

(Logue et al. 2009; Dochtermann 2010; Bell 2013). Carry-over effect may result in false short-term behavioural correlations; none was observed in our study, minimizing (tough not excluding) the possibility of carry-over effects (see 'Results').

The first test of male behaviour (Trial 1) was performed after approximately 1 wk of isolation. After all Trial 1 tests were completed, two females were added into 33 randomly assigned aquaria to create a female-biased social environment (FBE: 1 male, 2 females). In the remaining 32 aquaria, a single male and single female from the stock population were added to the focal male to create a male-biased social environment (MBE: 2 males, 1 female). The second test of focal male behaviour (Trial 2) was completed after approximately 5 wk of experience of the particular social environment (Fig. 1). Males had unrestricted access to females (and rivals in the MBE) and gained mating experience in their particular social environment. The treatment was maintained by replacing any dead female or non-experimental male. Focal males were not replaced; natural mortality of focal males caused a minor decrease in sample size during the second trials (FBE, n = 22; MBE, n = 17). Upon completion of Trial 2, males were returned to their treatment aquarium until their natural death.

Exploration Trials

Individual explorative behaviour was tested twice: at the age of approximately 19 wk (Exploration 1) and 31 wk (Exploration 2). We adopted a test of emergence from a refuge to study individual's exploration level, as commonly used in fish personality studies (e.g. Brown et al. 2005; Fabre et al. 2014). Trials took place between 09:00 and 17:00 Central European Time in a 43.5-l aquarium (70 × 25 × 25 cm), with three sides covered with opaque barriers to avoid disturbing the fish. The bottom of the aquarium was covered with a 1-cm layer of river gravel. The water depth was 5 cm and ambient temperature matched that of holding aquaria (23–25°C). The water was aerated, but aeration was paused during behavioural observations. Illumination was provided by a 25-W

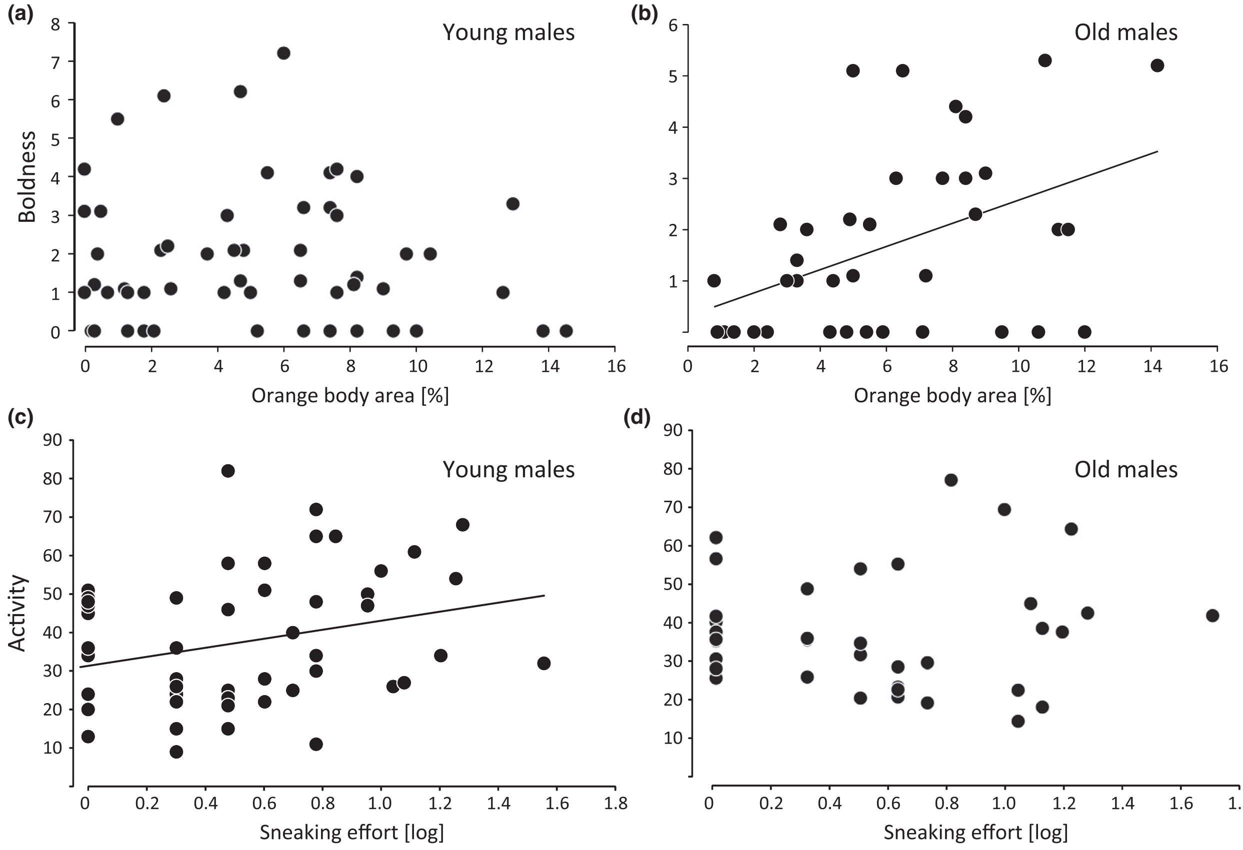

Fig. 1: Association between personality traits and male phenotypes. Relationship between area of orange coloration and boldness (number of predator inspection events) in young (r^2 = 0.005) (a) and older males (r^2 = 0.21) (b). Relationship between activity (number of zones crossed) and sneaking (number of sneaking attempts) in young inexperienced males (r^2 = 0.07) (c) and older males (r^2 = 0.004) (d).

Sun Glo daylight spectrum bulb positioned above the aquarium, which also received indirect natural daylight.

A randomly chosen focal male was placed in a refuge represented by a plastic box [16 (h) × 15 (w) × 8 (d) cm]. After 2 min, small doors (4.5 × 4 cm) were opened and the time taken to swim out from the refuge to the open arena by a full body length was recorded. Males that remained in the refuge for 10 min were considered as minimally explorative, and a score of 600 s was assigned to them.

Open Field Test: Boldness Towards Predator and General Activity

Individual levels of boldness and activity were tested at the age of approximately 20 wk (Boldness 1) and at the age of 32 wk (Boldness 2), that is in each case approximately 1 wk after the exploration trials. An open field test under the risk of potential predation was used to test individual behaviour towards predator and general activity. A slightly modified set-up from Frommen et al. (2009) was used. The same aquarium was used as in the exploration test (43.5 l, 70 × 25 × 25 cm with three sides covered with opaque barriers). The aquarium was divided by lines drawn on the front side into five compartments (0–4). Compartment 0 was the starting compartment, compartments 1, 2 and 3 were neutral, and Compartment 4 was the stimulus section with a fish predator. Compartments 0 and 4 were separated by glass dividers. The divider between compartments 3 and 4 was covered with a black opaque lid to prevent the predator from being seen; however, diffusion of predator olfactory cues was not prevented. Commercially obtained blue acara (*Andinoacara pulcher* (Gill 1858), Cichlidae), a generalized predator sympatric to *P. wingei*, was used as a potential predator. A male acara (total length 11 cm) was placed into Compartment 4 30 min prior to the onset of trials. Predator fish remained in a stable position and did not show any signs of stress or aggressive behaviour. A single individual of the blue acara was used across all replicates.

A randomly chosen focal male was gently released into Compartment 0 of the test aquarium. After 2-min acclimatization, the glass divider was lifted to allow free access to the test arena (compartments 0–3). At the same time, the opaque barrier covering divider of the predator compartment was lifted to allow visual contact with the predator. Focal male behaviour was scored using JWatcher 1.0 (Blumstein & Daniel 2007) for 10 min. The following behaviours were scored: percentage of time spent in each compartment, number of movements between compartments (a score of male activity) and number of individual inspection events towards the predator (boldness). Inspection events were defined as slow, hesitant moves by the focal male oriented towards the predator and were scored irrespective to the focal male position.

Courtship Behaviour Trials

Male mating behaviour was tested at the age of approximately 25 wk (Courtship 1) and 32 wk (Courtship 2). At Courtship 1, males were virgin and had no prior experience with an adult receptive female. Mating behaviour was scored in a 6-l aquarium with three sides covered with an opaque barrier to minimize disturbance. Light was provided by a 25-W Sun Glo daylight spectrum bulb positioned above the aquarium. Females used in the experiment were collected from a virgin female aquarium and left with a group of 3 adult non-experimental males from the stock aquarium for 1 d prior to the experimental trials to standardize their receptivity (Řežucha & Reichard 2014). During Courtship 2 trials (after exposure to social environment treatments), focal males were isolated from all conspecifics for 1.5 d prior to testing to standardize their mating effort. All replicates were completed between 09:00 and 16:00, that is later than 2 h after sunrise and 2 h before sunset.

A female was allowed to settle for 5 min in the test aquarium. Then, a randomly chosen focal male was released to the aquarium and left for 10 min to settle. After settling, male mating behaviour was scored for 15 min by a single observer using JWatcher 1.0. The number and duration of sigmoid displays (courtship), number of gonopodial thrusts (sneaking), number of gonopodial swings [loading gonopodium with sperm (Pilastro & Bisazza 1999)], number of gonopore nips [possibly analysing female cues (Herdman et al. 2004)] and general interest in females were scored. General interest was defined as time (in seconds) when male's head was oriented towards the female and there was a maximum distance of 10 cm between the male and female. After 15 min, the focal male was gently captured and returned to his home aquarium.

Photographing and Analysis of Colour Pattern

Focal males were photographed at the age of approximately 19 and 32 wk. A detailed description is given in Řežucha & Reichard (2015). In brief, a male was gently released into a photo-aquarium, fixed in a stable position against front glass and quickly photographed from both sides. A dark case and flash illumination were used to standardize conditions and a small ruler provided a scale. All pictures were taken in the shortest possible time, typically <4 min. Images were processed in Fiji (Schindelin et al. 2012) by measuring the area of carotenoid (light orange to dark red), melanin (dark black and fuzzy black) and iridescent (mostly green, blue, purple and silver, formed by guanine crystals in iridiophores) patches, and by counting the number of separate carotenoid and melanin spots. Each colour was expressed as a proportional area of lateral body projection (excluding eye, gonopodium and fins, with the exception of the caudal fin). The length of the lower and upper coloured part of the caudal fin (strap; black and carotenoid colour combined), gonopodium length, body length and length of the dorsal fin were also measured from the photographs. The measurement of morphological traits was completed blind with respect to behavioural data.

Data Analyses

All statistical analyses were performed in the R environment (R Development Core Team 2009). Repeatability was tested using intraclass correlation in the *psych* package, using ICC1 (standard repeatability *sensu* Lessells & Boag (1987)) and ICC3 (standardized for overall change in trait mean between time points, time treated as a fixed factor). For measures of personality traits that can only be expressed after emergence from the refuge (activity, boldness), the frequency of behaviour was expressed as a rate per unit time.

An information theoretical approach (Burnham & Anderson 2002) was used to test the effects of predictors on behavioural traits. A set of biologically plausible models was constructed, with various level of complexity. Before applying statistical models, data exploration was undertaken as recommended by Zuur et al. (2009). Collinearity among explanatory variables and among three response variables (personality traits) was tested using variance inflation factors (VIF). The VIF quantifies how much the variance increased due to collinearity among explanatory variables. Values of global variance inflation factor (GVIF) lower than 2–10 are considered to indicate an acceptable level of multicollinearity (Zuur et al. 2009). There was no collinearity (all GVIF < 3) among variables selected for model construction. Null models (i.e. intercept-only models) were always included, and the fit of predictor models (in the default *stat* package) was always compared with the null model. A total of 31 models of varying complexity were compared (Appendix 1). The models were selected on the basis of our hypotheses and their alternatives with a biological relevance. Where appropriate, Poisson (counts) and gamma (time) distribution (generalized linear models, GLM) and log-transformation to normalize data (linear models, LM) were considered to improve the fit of the models. Fits of alternative models (listed in Appendix 1) were compared using the Akaike information criterion corrected for small sample size (AIC_c) (*MuMIn* package). Model weights were calculated from relative likelihoods. Models within $\Delta AIC < 2$ were considered to have comparable support (Burnham & Anderson 2002). When the null model was included in the set of the best candidate models (i.e. within $\Delta AIC < 2$), models with predictor variables were considered to have no explanatory power. Only analyses where the null models were not within the set of the best models were considered further. If more than one parameterized model gained a support within $\Delta AIC < 2$, they were subjected to a model averaging procedure (using *MuMIn* package) and estimates from averaged models are presented. Original parameters of all models from the set of best models are presented in Table S1. In models within $\Delta AIC < 2$ (used for model averaging), the residuals were examined to ensure model assumptions were met. Models for Trial 1 and Trial 2 for each personality had identical structure but were treated separately.

The effect of male age on personality traits (pairwise difference in trait values between trials 1 and 2) was analysed using a paired *t*-test. The effect of social environment on personality traits (male-biased vs. female-biased, i.e. only data from Trial 2 for each trait) was compared using ANOVA. All p-values are for two-tailed test.

Results

All personality traits (exploration, boldness, activity) were significantly repeatable (Table 1a). Coloration and morphological traits were also highly repeatable across measurements, with a stronger repeatability when the ICC3 was used (i.e. accounting for population-level change in trait expression between trials 1 and 2) (Table 1b). Courtship behaviour, in contrast, was less repeatable. Only general male interest and gonopodial swings were repeatable. Sigmoid displays, sneaking attempts and gonopore nipping were not repeatable at all (Table 1c) because males responded to the change in their social environment (see Řežucha & Reichard 2014).

Table 1: Repeatability of male traits between the first and second trials

	ICC1	p	ICC3	p
(a) Personality traits				
Exploration	0.29	0.036	0.28	0.042
Inspection	0.39	0.006	0.39	0.007
Activity	0.38	0.007	0.38	0.009
(b) Morphological traits				
Orange coloration (%)	0.46	0.001	0.46	0.001
Black coloration (%)	0.30	0.033	0.32	0.023
Iridescent coloration (%)	0.09	0.703	0.37	0.009
Dot asymmetry	0.13	0.210	0.14	0.210
Orange dots (N)	0.67	0.001	0.73	0.001
Black dots (N)	0.43	0.004	0.41	0.005
Dorsal fin length	0.35	0.001	0.62	<0.001
Lower sword length	0.69	<0.001	0.76	<0.001
Upper sword length	0.60	<0.001	0.86	<0.001
Gonopodium length	0.91	<0.001	0.91	<0.001
Total length	0.77	<0.001	0.78	<0.001
Standard length	0.85	<0.001	0.85	<0.001
(c) Mating behaviour traits				
General interest	0.32	0.018	0.37	0.008
Gonopodial swings	0.28	0.026	0.29	0.032
Gonopore nipping	0.15	0.170	0.17	0.140
Sigmoid display duration	−0.19	0.900	−0.39	0.600
Gonopodial thrusts	−0.01	0.520	−0.01	0.570

ICC1 is standard repeatability *sensu* Lessells & Boag (1987) and ICC3 denotes repeatability standardized for overall change in population trait mean between time points.

Table 2: Model-averaged estimates (and their SE) from the top models (by >2 AIC) and their statistical significance for (a) boldness towards predators in older males and (b) activity of young males

	Estimate	SE	*z*-score	p Value
(a) Boldness of old males				
Intercept	−0.402	0.297	1.31	0.191
Sigmoid displays	0.028	0.013	2.07	0.039
Percentage of orange	0.103	0.042	2.38	0.018
(b) Activity of young males				
Intercept	21.088	28.641	0.73	0.469
Gonopodial thrusts[a]	4.949	2.270	2.13	0.033
Total length	1.574	1.759	0.87	0.383

[a] log(x + 1)-transformed prior analysis.

There was no BS. Personality traits were not associated with each other (Pearson correlation: exploration and boldness: $r = -0.094$, p = 0.482; exploration and activity: $r = -0.111$, p = 0.406; boldness and activity: $r = -0.147$, p = 0.272).

Male exploration (time to emergence from hide) was not associated with any morphological or courtship traits; the null model had highest explanatory power (Appendix 1). Male age (paired *t*-test, $t_{36} = 0.55$, p = 0.59) and social environment (log-transformed, $F_{1,36} = 0.82$, p = 0.37) had no effect on male exploration.

Male boldness towards the predator was not associated with any morphological or courtship trait in young males (Appendix 1). In older males (Trial 2), more carotenoid coloration (Fig. 1a) and a higher tendency to court females were positively associated with boldness towards predators (Table 2a). Male age (paired *t*-test, $t_{36} = 0.87$, p = 0.39) and social environment ($F_{1,36} = 0.33$, p = 0.57) had no effect on male propensity to inspect predator (decrease by ΔAIC 1.5–3.0 for paired comparisons between otherwise identical models), implying that social treatment did not affect male boldness levels.

In young males, activity was positively associated with the rate of sneaking (Fig. 1b); the effect of male size was retained in the final averaged model (Appendix 1), but was not significant (Table 2b). This association ceased in sexually experienced males (Fig. 1d, Appendix 1). Male age (paired *t*-test, $t_{36} = 0.33$, p = 0.75) and social environment (log-transformed data, $F_{1,36} = 0.01$, p = 0.93; decrease by ΔAIC 1.5–3.0 for paired comparisons between otherwise identical models) had no effect on male activity level.

There was no population-level change in any personality trait values between young and old males (exploration: $F_{1,32} = 0.16$, p = 0.69, boldness: $F_{1,32} = 0.03$, p = 0.83, activity: $F_{1,32} = 0.21$, p = 0.65). A temporal change in courtship behaviour (and its response to social environment) has been reported elsewhere (Řežucha & Reichard 2014).

Discussion

Repeatable Behaviour But a Lack of BS

All personality traits (exploration, boldness towards predator, general activity) of male *P. wingei* were highly repeatable despite the change in social environment during the 3 mo of the study. This finding is consistent with data on personalities in the closely related *P. reticulata* (Budaev 1997; Smith & Blumstein 2010; Brown & Irving 2014) and other taxa (Bell et al. 2009). At the same time, no BS was detected, suggesting the independence of different personality traits in focal males. This is surprising, because BSs encompassing boldness towards predator, refuge use and activity are common (e.g. Mazué et al. 2015; Wilson & Godin 2009 but see McEvoy et al. 2015), and hiding in a refuge is a form of protection and a certain level of boldness is needed to leave the refuge and start exploration. Behavioural syndromes are often linked with aggression to conspecifics and appear to be promoted by the same underlying mechanisms (Caramaschi et al. 2013), responsible for the coupling of behavioural traits, including reproductive behaviour (Mutzel et al. 2013). This enables females to judge male's mating or parental quality (Barnett et al. 2012; Stein & Bell 2012). However, particular BSs can also increase male reproductive success irrespective of female choice (Sih et al. 2014). While we suggest that the lack of correlation between exploration and boldness towards predator in our data set was a real phenomenon, it is possible that larger sample size (Garamszegi et al. 2012) or inclusion of positional data during predator inspection events and their use in the analysis would strengthen the association.

Our findings underscore strong context-specific differences in boldness (Coleman & Wilson 1998). The boldness needed to emerge from a safe refuge was unrelated to the boldness needed for gaining information about a potential threat in *P. wingei*. Similarly, Carter et al. (2012) did not observe any relationship between response to a threatening stimulus (snake) and reaction to a novel object (new food item) in wild chacma baboons (*Papio urcinus*). We also did not record any association between exploration and general activity level, despite frequent correlation between them reported elsewhere (e.g. Fraser et al. 2001; Sih et al. 2004; but see Conrad et al. 2011; Sinclair et al. 2014). It is possible that the link between exploration and activity is adaptive only in certain environments and under particular circumstances. Both exploration and activity are also prone to be strongly state dependent, implying the existence of such an association only under specific conditions, such as low energy reserves (Wolf & Weissing 2010). Individual behaviour also seems to be largely influenced by the presence of predators, which may promote behavioural correlations on the one hand (Bell & Sih 2007) and uncover behavioural flexibility on the other (David et al. 2014). One caveat of our study was that our measure of activity level was not independent of boldness towards predator, potentially resulting in a false significant association. However, these two behaviours were not correlated in our study.

Another reason for the lack of correlations among personality traits may stem from the paucity of selective pressure in captivity (Archard & Braithwaite 2010), with predation risk being considered a major source of personality trait correlations (Bell 2005; Bell & Sih 2007). Domestication has a clear effect on fish behaviour (Metcalfe et al. 2003; Huntingford 2004) and may have therefore also affected the outcome of this study. Experimental males were kept in a predictable environment without predation or other external sources of mortality for several generations, similar to that of domestic strains. While Bleakley et al. (2006) demonstrated that individuals of inbred *P. reticulata* strains retained the capacity to respond appropriately to predator cues, we acknowledge that a lack of BS may arise from relaxed selection in a benign captive environment.

No Effect of Social Environment on Male Personality

Social environment did not affect individual male personality over the period of 5 wk, leading to the conclusion that it has limited impact on personality traits modulation, contrary to, for example, abiotic factors (Sinclair et al. 2014). This result corroborates the finding of overall relative stability of individual personality traits despite changes in surrounding social conditions, such as reported in the water strider *Aquarius remigis* (Sih & Watters 2005). In contrast, sex ratio affected individual boldness in *P. reticulata* males who were bolder in male-biased than in female-biased groups (Piyapong et al. 2010). Nevertheless, Piyapong et al.'s (2010) study tested only the actual level of boldness in various contexts, without taking individual experience or ontogenetic changes into account.

Personality, AMB and Morphological Traits

There was some association between personality and AMB. In young virgin males, more active individuals were more likely to attempt sneak copulations than less active individuals. This is consistent with the link between male activity levels and mate searching. Sneaking is less time- (Parker 1974) and energy (Sargent 1985)-consuming than courtship, and sneaker males can spend more time and energy on searching and chasing females to sneak copulations. Among older males, individuals with a larger proportion of orange, carotenoid-based coloration had a higher tendency to court females and were bolder towards predators, as has been found in male *P. reticulata* (Godin & Dugatkin 1996). Guppy males with brighter coloration are, as in many other taxa, considered to be more viable due to higher intrinsic quality (Godin & McDonough 2003; Locatello et al. 2006), preferred by females for solicited matings (Alexander & Breden 2004), but also preferentially targeted by predators (Godin & McDonough 2003). Male courtship is costly and makes males conspicuous to predators. Brighter males can therefore invest in predator inspection and acquire information about potential threats and hide or, alternatively, deter predator attacks (Dugatkin & Godin 1992). The link between courtship and boldness towards predator was only manifested in older males. It may be speculated that social experience, in terms of interaction with females, is needed to properly develop boldness in courting colourful males.

The morphological traits tested (gonopodium length, body length, coloured caudal straps length and length of dorsal fin) were not important in determining individual choice of AMB in *P. wingei*. This contrasts with a positive correlation between gonopodium length and number of gonopodial thrusts reported for *P. reticulata* (Reynolds et al. 1993), although the association was only apparent under low light conditions. Similarly, Karino & Kobayashi (2005) reported a positive link between the rate of gonopodial thrusts and caudal fin length in *P. reticulata*. The difference may simply reflect variation among populations with variable selection regimes. Alternatively, the lack of correlation between AMB and morphological traits in *P. wingei* despite their presence in some *P. reticulata* populations may arise from slight differences in their mating behaviour (Poeser et al. 2005) and lower level of intra- and intersexual aggression in *P. wingei* males.

Conclusion

Personality traits of *Poecilia wingei* males were highly repeatable, despite no BS being identified. There was no general difference in any personality trait between Trial 1 and Trial 2 or between the two social environments, that is living with a rival, or females did not make males bolder, more explorative or more active. Young active males were more likely to attempt sneak copulations. Among older fish, more orange, courting males were more likely to inspect predators irrespective of their social environment – but in virgin males this was not observed. The resulting temporal change of individual AMB in the course of 5 wk and relative stability of personality traits suggest higher flexibility of AMB. It seems that personality traits are relatively fixed in a short timescale compared with more flexible AMB. It is notable because a dramatic change in the social environment was predicted to at least slightly influence the expression of personality traits assuming that different traits are favoured in different environments. As a result, social environments in this experiment only influenced AMB while personality traits remained unchanged. Taken together, our results suggest that AMB is independent of personality traits as there was no personality characteristic predisposing males to adopt either courting or sneaking as a general strategy.

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Conflict of interest

The authors declare no conflict of interest.

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Appendix 1: Set of all candidate models, their degrees of freedom (df), their relative fits as compared to the best fitting model (ΔAIC) and their relative eight (*w*) for each personality trait. The best fitting models are indicated in bold. In cases where a model other than the null model was the best fitting, other models with ΔAIC < 2.0 (used in the model averaging) are also indicated in bold.

		Emergence from refuge				Boldness towards predator				Activity levels			
		Young males		Older males		Young males		Older males		Young males		Older males	
Model parameters	df	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*
Null model (intercept-only)	2	**0.00**	**0.13**	**0.00**	**0.12**	0.58	0.08	12.54	0.00	2.56	0.06	**0.00**	**0.11**
Orange %	3	2.11	0.04	1.41	0.06	2.23	0.03	**1.87**	**0.09**	4.55	0.02	1.39	0.06
Orange % + Total length	4	4.26	0.02	3.03	0.03	2.76	0.03	4.20	0.03	5.90	0.01	3.38	0.02
Total length	3	2.05	0.05	1.58	0.05	1.05	0.06	14.78	0.00	3.80	0.03	1.81	0.05
Orange % + Black % + Total length	5	4.01	0.02	5.21	0.01	5.07	0.01	5.88	0.01	8.29	0.00	6.02	0.01
General interest	3	2.03	0.05	1.86	0.05	2.13	0.03	12.00	0.00	4.77	0.02	0.65	0.08
Sigmoid displays	3	1.10	0.07	1.06	0.07	1.32	0.05	3.00	0.05	4.33	0.03	2.36	0.04
Gonopodial thrusts	3	1.21	0.07	2.21	0.04	2.70	0.03	14.67	0.00	**0.00**	**0.22**	2.22	0.04
Gonopodial swings	3	0.94	0.08	1.28	0.06	2.00	0.04	12.40	0.00	3.71	0.04	2.15	0.04
Gonopore nibs	3	1.72	0.05	0.83	0.08	0.75	0.07	14.64	0.00	2.61	0.06	2.35	0.04
General interest + Total length	4	4.26	0.02	3.75	0.02	3.04	0.02	14.37	0.00	5.87	0.01	2.65	0.03
General interest + Orange %	4	4.25	0.02	3.30	0.02	3.80	0.02	4.05	0.03	6.84	0.01	2.83	0.03
General interest + Orange % + Total length	5	6.58	0.00	5.25	0.01	4.80	0.01	6.54	0.01	8.04	0.00	4.99	0.01
Sigmoid displays	4	3.07	0.03	2.42	0.03	1.29	0.05	5.35	0.02	5.44	0.01	4.32	0.01
Sigmoid displays + Orange % + Total length	5	5.37	0.01	3.94	0.02	2.98	0.02	2.40	0.07	7.64	0.00	5.88	0.01
Sigmoid displays + Orange %	4	3.30	0.02	2.56	0.03	3.00	0.02	**0.00**	**0.22**	6.41	0.01	3.74	0.02
Gonopodial thrusts + Total length	4	3.30	0.02	3.90	0.02	3.26	0.02	17.03	0.00	**1.50**	**0.11**	4.03	0.02
Gonopodial thrusts + Orange %	4	3.29	0.02	3.66	0.02	4.37	0.01	3.82	0.03	2.28	0.07	3.79	0.02
Gonopodial thrusts + Total length + Orange %	5	5.49	0.01	5.39	0.01	5.01	0.01	6.33	0.01	3.88	0.03	5.81	0.01
Gonopodium length	3	1.85	0.05	1.93	0.04	0.00	0.10	14.76	0.00	4.54	0.02	2.24	0.04
Gonopodial thrusts + Gonopodium length	4	3.23	0.03	4.22	0.01	2.18	0.03	17.02	0.00	2.21	0.07	4.64	0.01
Gonopodial thrusts + Gonopodium length + Total length	5	5.55	0.01	6.21	0.01	2.96	0.02	19.53	0.00	3.49	0.04	6.38	0.00
Gonopodium length + Total length	4	4.11	0.02	3.81	0.02	0.66	0.07	17.12	0.00	5.40	0.02	3.95	0.02
Black %	3	1.26	0.07	1.64	0.05	2.62	0.03	10.50	0.00	4.40	0.02	2.11	0.04
Black % + Total length	4	3.18	0.03	2.99	0.03	2.98	0.02	12.86	0.00	5.92	0.01	4.10	0.01
Iridescence	3	2.24	0.04	1.04	0.07	1.21	0.06	11.95	0.00	4.58	0.02	2.33	0.04
Iridescence + Total length	4	4.37	0.01	3.00	0.03	2.28	0.03	14.20	0.00	5.76	0.01	4.32	0.01
Orange % + Black % + Iridescence + Total length	6	6.47	0.00	7.49	0.00	6.92	0.00	8.47	0.00	10.62	0.00	8.62	0.00

Appendix 1: (Continued)

		Emergence from refuge				Boldness towards predator				Activity levels			
		Young males		Older males		Young males		Older males		Young males		Older males	
Model parameters	df	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*
Orange % + Black % + Total length + Sigmoid displays	6	5.56	0.01	6.33	0.00	5.39	0.01	5.03	0.02	10.07	0.00	8.62	0.00
Orange % + Black % + Total length + Gonopodial thrusts	6	5.09	0.01	7.68	0.00	7.41	0.00	8.11	0.00	6.26	0.01	8.64	0.00
Orange % + Black % + Total length + Sigmoid displays + Gonopodium length	7	8.09	0.00	8.84	0.00	4.81	0.01	7.87	0.00	12.41	0.00	11.53	0.00
Orange % + Black % + Total length + Gonopodial thrusts + Gonopodium length	7	7.72	0.00	10.86	0.00	17.57	0.00	10.45	0.00	8.62	0.00	11.47	0.00

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Model parameters, their standard errors (SE), *z*-values and their statistical significance (p) for the set of best fitting models (deltaAIC < 2).