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ORIGINAL ARTICLE

Male guppies differ in daily frequency but not diel pattern of display under daily light changes

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Abstract

Sexually signalling animals must trade off the benefits of attracting mates with the consequences of attracting predators. For male guppies, predation risk depends on their behaviour, colouration, environmental conditions and changing intensity of predation throughout the day. Theoretically, this drives diel patterns of display behaviour in native Trinidadian populations, where males display more under low-light conditions when their most dangerous predator is less active. Here, we observed Australian guppies in a laboratory setting to investigate their diel display pattern, and if this pattern is controlled by ambient light intensity. We also quantified individual variation in both the daily frequency and diel pattern of displays, and if such variation relates to body size, colouration and a non-sexual behaviour. Under a typical daily light regime, male guppies displayed mostly in the first hour of observation. Extending the duration of dawn-like lighting, however, resulted in an extended period of high display, demonstrating that light intensity per se is an important cue for this behaviour. These findings mirror those obtained for Trinidadian populations, suggesting that male courtship timing is likely shaped by broad, potentially generalizable features of guppy ecology. The effect of acclimation to captive conditions on male behaviour is also discussed. Whereas the temporal pattern of display appeared consistent, individuals varied in their daily display frequency, and this was correlated with variation in colour phenotype and a measure of non-sexual risk acceptance behaviour. Such relationships pose promising avenues for integrating behavioural and sensory ecology with contemporary work on behavioural syndromes and animal personality.

Significance statement

To limit the costs of their conspicuous colour patterns, male guppies should alter their behaviour to avoid predation. However, our understanding of how different individuals deal with this problem is lacking. Following individuals in the laboratory, we demonstrated individual variation in the daily frequency of male displays, and this was correlated with variation in colour phenotypes and non-sexual behaviour. However, all male guppies displayed more in the early hours of the day and extending the period of low lighting also extended this period of elevated display. These findings replicate and expand experiments on native populations, suggesting that male courtship timing is likely shaped by broad, potentially generalizable features of guppy ecology.

Keywords Animal behaviour · Mating behaviour · Light environment · Trade-off · Sexual signal · Colour

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Introduction

Sexual communication involves some of the most striking behaviours in the animal kingdom, and both signals and their individual components present opportunities to study opposing selection pressures. For visual signallers, the classic dilemma is how to appear conspicuous to conspecifics of the opposite sex yet escape the attention of predators (Endler 1987). The evolutionary consequence of this trade-off has been well demonstrated in the guppy, *Poecilia reticulata*, which is a model organism for understanding signal evolution and is well

suited to laboratory and field study. Male guppies are heavily adorned with colour, and court females using highly ritualised visual displays (Houde 1988). Females prefer males with more colourful signals (Godin and Dugatkin 1996), but brighter males are thought to experience higher predation risk (Millar et al. 2006), thus placing males under two competing evolutionary pressures. This trade-off is reflected in the natural variation present in the species, where guppy populations under higher predation are less colourful than those living without predation, and also by manipulative evolution experiments in which guppy populations have been shown to evolve to be more colourful if transplanted into a lower-predation habitat (Endler 1980; Kemp et al. 2009).

There are various morphological and behavioural solutions for reducing conspicuousness to predators, but the primary strategy that has been investigated in guppies is context-dependent signalling behaviour. Guppies can switch from conspicuous sigmoid displays to attempting less conspicuous sneak copulations. Evans et al. (2002) found that experimentally showing predators to female guppies led to a shift from sigmoid displays to sneak copulation attempts in male guppies, even though the males themselves could not see the predators. However, sneak copulations average three times less sperm delivered compared to mating after courtship (Pilastro and Bisazza 1999), so there is evolutionary pressure for males to display to females.

Guppies have higher display frequencies early in the day when light intensity is lower and their predators are less active and minimise their display behaviour later in the day under the opposite conditions (Endler 1987). Endler (1987) investigated the diel patterns of guppy display and sneak behaviour with and without predators in an artificial river (guppies were originally sourced from Trinidad and Venezuela). He found that, in both cases, males displayed more in dusk and dawn conditions, but that this pattern was amplified when predators were introduced. However, sneak behaviour remained consistent across the day, meaning guppies invest relatively more into sneak behaviour under high ambient light levels. Supporting this, Endler showed that *Crenicicla frenata* (formerly *C. alta*), generally considered the guppy's most dangerous predator, was most active during the day, and proposed that diel display behaviour has been strongly shaped by predation. Archard et al. (2009) found that fish from the Aripo and Quare rivers exhibited a similar pattern of diurnal display, even despite differing daytime predator regimes. Compared to fish from the low-predation Aripo site, guppies from the high-predation Quare site showed a stronger diel pattern with higher display frequencies in the low light and lower display frequencies in the high light. However, unlike the findings of Endler (1987), there were more sneak copulations during low-light periods of the day. This pattern did not significantly vary between populations. For display behaviour in Trinidadian guppies, Reynolds et al. (1993) and Archard et al. (2009) both found that this effect can be experimentally separated from time of day and replicated by manipulating light levels alone. Neither Archard et al. (2009) nor Reynolds et al. (1993) found that male sneak behaviour varied under experimentally manipulated light levels.

Population-level differences exist in both learnt and innate guppy behaviours, such as predator response, schooling behaviour, and female preference (Houde 1988; Magurran and Seghers 1990). Guppies originate from the northeast mainland and islands of South America, but invasive populations have been established in many countries (Deacon et al. 2011). In Australia, there are several established feral populations (Lindholm et al. 2005), of which the Alligator Creek population has been used extensively in research (e.g. Brooks and Endler 2001; Mariette et al. 2006; Evans and Kelley 2008). This population was most likely founded by fish introduced from Guyana (Lindholm et al. 2005), where—as in Trinidad—the main guppy predator is a day-hunting pike cichlid, *Crenicichla saxatilis* (Johansson et al. 2004). Feral populations elsewhere around the world will, however, coexist with greatly varied and novel predatory communities, and potentially experience stronger predation from terrestrial species such as birds. Few studies have investigated whether and how the timing of guppy courtship varies under novel conditions, and it remains unknown for otherwise important study populations such as Australian Alligator Creek fish. It is likewise unknown whether any daily patterns of courtship in such populations are controlled at the proximate level by variation in light intensity as shown for Trinidadian populations (Reynolds et al. 1993; Archard et al. 2009).

If populations differ in their diel schedules, do individuals also differ within those populations? Guppies present incredible diversity in many areas that could lead to individual diel patterns. Firstly, male guppies differ in the frequencies that they display and attempt sneak copulations, and females use variation in male display frequencies as an indicator of mate quality (Nicoletto 1993; Matthews et al. 1997). Differences in male display frequency have been linked to sperm quality (Matthews et al. 1997), ornament complexity, orange spot size/coverage, swimming performance (Nicoletto 1993), tail size (Bischoff et al. 1985) and body size (Rodd and Sokolowski 1995; although see Magellan et al. 2005), which themselves all vary significantly within populations. Differences in male sneak frequency have been linked to sperm quantity (Matthews et al. 1997), orange area (Nicoletto 1993), body size (Magellan et al. 2005) and tail length (Karino and Kamada 2009). Interestingly, the relationship to body size demonstrates a similar trade-off to colour: large males display more under low predation and small males display more under high predation even when adjusted for size difference between low- and high-predation communities (Rodd and Sokolowski 1995). Male guppies differ dramatically in colouration, even within populations, with entire colour

types being present and absent on different males, and populations differing considerably in their average colour representations (Endler and Houde 1995; Kemp et al. 2009). However, orange is the only aspect of guppy colouration that has been related to the frequency of display or sneak attempts, where both are correlated with orange coverage (Nicoletto 1993). Individuals also vary in important behavioural traits, such as their predator tolerance and antipredator behaviour, and other personality types (Dugatkin 1992; Godin and Dugatkin 1996; Harris et al. 2010). Males vary in their preferences for female traits (Dosen and Montgomerie 2004), and females in their preference for male traits (Houde 1988, 1994; Endler and Houde 1995; Godin and Dugatkin 1995; Brooks and Endler 2001). Given the evidence for high within-population diversity in many other behaviours, it is possible—if not likely—that individual males also vary in their diel display patterns. This is important to explore because it presents an avenue by which differentially ornamented males could adjust their fitness expectation under the trade-off between natural selection and sexual selection (i.e. predation risk versus courtship success; see below for specific treatment of this point).

Interestingly, there has been little investigation into the potential relationship between non-sexual behavioural (personality) traits and sexual behaviour. Behavioural syndromes force traits to evolve in groups, rather than in isolation, which can generate otherwise unpredicted trade-offs across contexts and therefore have critical implications for our understandings of evolution and ecology (Sih et al. 2004, 2012; Stapley and Keogh 2005). They can also serve as important maintainers for individual variation, in some cases leading to clear behavioural types within a syndrome (Sih et al. 2004, 2012). Behavioural types have been linked to fitness traits. For example, male three-spined sticklebacks, *Gasterosteus aculeatus*, that are bolder towards predators also obtain better breeding sites through aggression (Huntingford 1976). In the southern water skink, *Eulamprus heatwolei*, individuals that are territorial have increased aggression and reduced exploration, and territorial males sire more offspring while exploratory males and females produce larger offspring (Stapley and Keogh 2005). It is in these ways that variation in non-sexual behaviour is thought to impact on fitness. However, variation in these traits may be linked to fitness directly if sexual behaviours form part of these syndromes. To our knowledge, Kelley et al. (2013) is the only study to have investigated a link between courtship behaviour and non-sexual behaviour, finding no evidence of a link between exploratory and courtship behaviour. The shyness/boldness behavioural types, representing individual differences in traits such as spatial use (Kotrschal et al. 2014), predator tolerance (Godin and Dugatkin 1996), predator inspection (Godin and Dugatkin 1996) and post predator recovery time (Heathcote et al. 2017), may be linked with sexual behaviour in guppies if these behaviours are as driven by predation as we think. For example, bolder males may continue to display when less shy males switch to sneak copulation tactics under predation risk.

Here, we aimed to investigate the influence of daily light regimes and individual variation upon male sexual behaviour in a feral Australian guppy population. To do this, we first observed guppies under an artificial light programmed with a 'natural' lighting schedule where the light intensity peaked at midday and declined symmetrically towards dusk and dawn. This allowed us to investigate if male Alligator Creek fish showed a similar diel pattern of displays as reported for Trinidadian populations (and as is also likely for their Guyanese ancestors). We also recorded sneak copulation attempts, as they are thought to provide males a lower-risk alternative to displays (Endler 1987). We then manipulated the light schedule to present the population with a considerably extended dusk period. This allowed us to separate the effects of time and light to investigate the hypothesis that ambient light levels provide the proximate cue for diel display variation in our population (sensu Archard et al. 2009). Specifically, this hypothesis predicts that prolonging the period of dawn-like lighting should prompt a more extended period of high-display activity. Clear a priori predictions for male sneak behaviour under varying light conditions are difficult to formulate due to contradictory findings in the literature (Endler 1987; Archard et al. 2009). However, observations on guppies removed from their native rivers in these experiments did not find a relationship between light intensity and sneak attempts, suggesting that we may not find an effect.

Aside from population-level data, this study was also designed to generate detailed data on each male subject's daily pattern of display and sneak behaviour. We sought this to examine whether there was consistent individual variation regarding the overall intensity and/or diel timing of sexual activity. To this end, the study design prioritised a solid characterisation of behaviour among a select sample of individuals (n = 10) as opposed to a less stringent assessment across a broader spread of males. Despite the low statistical power thus afforded, we nevertheless also took the opportunity to explore individual-level relationships between sexual activity, ornamental colouration and non-sexual behaviour. In terms of ornamentation, the most straightforward general prediction is that more heavily and/or strikingly (diversely) ornamented males should curtail active display behaviour more sharply as the risk of predator detection increases. The greater visual conspicuousness of such individuals may bestow a competitive sexual advantage when predators are scarce yet predispose them for disproportionate risks at other times. We therefore expected that more 'colourful' males (see 'Materials and methods') should display under more restricted circumstances, and that this should apply consistently under both 'natural' and 'extended dawn' experimental treatments. Second, we measured each individual's latency to emerge

from a shelter to investigate any link between courtship activity and a putative non-sexual measure of risk acceptance. This assay is part of a suite of assays used to assess a feature of behaviour termed 'boldness' or 'exploration' across a breadth of animals (e.g. Brown et al. 2007; Kortet and Hendrick 2007; Chapman et al. 2011; Kerman et al. 2016), and measures highly repeatable behavioural differences in guppies (O'Neill et al. 2018). Boldness is thought to reflect an animal's reaction to threatening or dangerous environments (Beckmann and Biro, 2013). If fear of predators drives the diel pattern, then we predict that fish with low emergence times will display at higher frequencies under higher ambient light intensity. Females are known to prefer 'bolder' males (Godin and Dugatkin 1996), but to our knowledge, no research has yet investigated the possible links between boldness, colour and display frequency.

Materials and methods

Sampling site

Adult male and female guppies were collected from Alligator Creek in Queensland, Australia, in early December 2017 to generate offspring for another experiment. Alligator Creek is located within the Bowling Green Bay National Park (19.4239° S, 146.9456° E). The creek fluctuates heavily in flow rate across the dry and wet seasons but, at a median water level, presents a series of rocky pools and riffles gradually increasing in size with decreasing elevation. The marbled eel (*Anguilla* sp.) and jungle perch (*Kuhlia rupestris*) are the main predators in the area that are thought to prey upon guppies (Lindholm et al. 2014). However, guppies appear to persist in the upper pools where predators are absent and were not present in the pools where predators were visible when we were sampling. It is difficult to predict how guppies and their predators disperse in flooding periods. Guppies were relocated to our laboratory at Macquarie University and housed in groups in large 125-L (90 × 35 × 50 cm) stock breeding tanks. Guppies were reportedly introduced to this site over 65 years ago to aid in mosquito control (Brooks and Endler 2001; Lindholm et al. 2005) and are thought to have been sourced from a guppy population in Guyana (Lindholm et al. 2005).

Light manipulation trials

Approximately 2 weeks after collection, we moved 30 fish (15 males and 15 females) to a 125-L (90 × 35 × 50 cm) tank, kept at 27 °C (± 1 °C). This allowed for an even sex ratio, and for spare males in the case of deaths during the acclimatisation period or early observations. Although observing guppies in group settings can cause issues with sample independence, it best represents a natural courtship setting where males and females have a choice between many individuals and males are free to compete with each other. This method has been previously used to address diel courtship behaviour in guppies (Endler 1987; Archard et al. 2009). The tank bottom was lined with substrate composed of sand and rocks of various small sizes, as well as a light amount of foliage (java fern *Microsorum pteropus* and java moss *Vesicularia dubyana*) to provide some shelter without obscuring the observer view of the tank. Black cardboard lined the tank on the sides and rear. An Aqua Illumination 'Hydra 52' LED aquarium light (Aqua Illumination, USA), was programmed to turn on at 0700, ramp up to a peak at 1200 and then ramp down and turn off at 1700 (Fig. 1). This represented a compressed version of light conditions in the field, where the sun rises at approximately 0500, peaks at 1200 and sets at 1900 in the summer months (Hoffmann, 2017). Fish were then given 2 weeks to acclimatise to these conditions.

We collected 5 days of observational data for each 12 males using the focal-animal method, during the period of January to March 2018. The observer (SON) sat still in front of the tank with the room lights turned off and would observe a fish for 5 min, recording the number of sigmoid displays and sneak attempts, before moving to the next fish. In this way, six fish could be observed on the hour, seven times, from 0800 to 1430 and 5 days of hourly data could be generated for all 12 fish over 10 days of observations.

Once this round of observations concluded, the light schedule was altered to give the tank a greatly extended 'dawn' period (Fig. 1). The light turned on at 0700, peaked at 1400 and quickly declined and turned off at 1700. Guppies were given 1 week to adjust to the new light schedule and then observations were carried out, following the same procedure described above, over the following 2 weeks.

On observation days, fish were fed only after all observations were finished for the day (on other days, fish were fed ad libitum). Individual males are identifiable by their natural colour variation and no tagging was necessary. Male guppies present their colour patterns to females with sigmoid displays, where they arch their spine to form an 'S' shape and quickly move back and forth, although they may also try to chase and perform non-consensual 'sneak' copulations (Houde 1997).

It was not possible to record data blind because our study involved focal animals that were tracked according to colour patterns.

Colour measurement

We quantified the occurrence and areal coverage of male ornamentation using digital photography. Live test subjects were anaesthetised with a 1-mg/L solution of MS-222 buffered with sodium bicarbonate and photographed on both left and right sides against a white and black background. The total out-of-water handling for each fish was ca. 60–90 s. The white

background best presents black and orange colouration, while the black background best presents iridescent colouration (Kemp et al. 2009). A Canon EOS 600D camera was fixed directly overhead, and the guppies were illuminated by a small (60 lumen) LED light angled down at 45°, at a distance of approximately 20 cm. A ruler was placed in frame for each photograph to determine scale. We traced the total body area and the areal coverage of three main colour classes (black, orange, iridescent blue/green) on each photograph using Adobe Photoshop CC (version CC 2018 19.1.3). These colour components can be spectrally described as follows: black: < 5% reflectance across the 300–799-nm range; blue: Gaussian-type reflectance function with peak ca. 400 nm; green: Gaussian-type reflectance function with a peak ca. 515 nm; and orange: sigmoidal-type reflectance with an inflection point ca. 580 nm (Kemp et al. 2009).

This provided an area in pixels which was then converted into square millimetres. We averaged the colour areas on the left and right sides of the guppies to account for colour asymmetry.

Given that there is great complexity in how to best judge perceived colour signal conspicuousness (Endler 1990; Kemp et al. 2015), we summarised our data in terms of two well-established summary measures for guppies (Endler 1978). Colour area (C_A—the overall proportion of ornamented area to total lateral body area) and colour diversity (C_D—the 'evenness' to which the three main classes are represented) were calculated according to the respective formulae:

$$C_A = \frac{(Bl + Or + Irid)}{Body}$$

$$C_D = \frac{1}{\left(Bl^2 + Or^2 + Irid^2\right)}$$

where 'Bl', 'Or' and 'Irid' refer to the lateral area of black, orange and iridescent markings, and 'Body' refers to total lateral body area (excluding the caudal fin).

Emergence assays

Two of the original 12 test subjects expired prior to the end of behavioural trails; hence, the remaining ten males were run through an emergence assay. The apparatus consisted of a bare-bottomed 90-L tank (51 × 92 × 21 cm) filled to a depth of 9 cm with water sourced from the stock tank, with a starter box placed at one end. The starter box was an open-roofed, black plastic container lined with gravel, with a sliding door facing the centre of the tank. Although open, the starter box blocks the line of sight to the observer and partially reduces ambient light levels. Emergence time should represent time taken for a guppy to emerge from a sheltered environment into an open and somewhat aversive environment, which may indicate a bold/shy behavioural type. This door was opened remotely, and the tank observed by an observer off to one side.

Males were isolated in plastic cups for ca. 1 h prior to testing. They were then placed in the closed chamber to acclimate for 10 min prior to raising the chamber door. Ten minutes of acclimation has been found to produce emergence behaviour most indicative of overall behavioural types in guppies (O'Neill et al. 2018). Latency to emerge was measured to the nearest 1 s using a digital stopwatch.

Statistical analysis

We assessed the effects of individual and time of day and the impact of light treatment upon male display behaviour using a generalised linear mixed model (GLMM) with a Gaussian response and identity link function. We fitted a model with display number as the dependent variable, individual ID as a random variable, hour and treatment (light environment) as main effects and date as a covariate to account for habituation over the trial. Date was simply the number of days following the beginning of the experiment. We included this to account for any consistent changes over time due to, for example, acclimatisation to the laboratory conditions or increases in age. We also included second- and third-order interaction terms involving individual ID, hour and treatment. To test the significance of effects in mixed or random models, error terms must be constructed that contain all the same sources of random variation except for the variation of the respective effect of interest. Here, we use Satterthwaite's method of denominator synthesis (Satterthwaite, 1946), which finds the linear combinations of sources of random variation that serve as appropriate error terms for testing the significance of the respective effect of interest.

Due to an excess of zero counts in the sneak data, as confirmed by a Vuong test (Vuong 1989), we used a zero-inflated generalised linear mixed model with a Poisson distribution and log-link function to assess the effects of individual and time of day and the impact of light treatment on male sneak behaviour. We included the same conditional and random terms as in the GLMM of daily display frequency, above, as well as a single zero-inflation parameter for all observations and fit it using the 'glmmTMB' package (Brooks et al. 2017) for R (v 3.5.2; R Core Team 2018).

Finally, we assessed potential individual-level relationships between sexual activity and body size, ornamental colour traits and emergence via univariate correlation analyses. We opted not to attempt a multivariable model fitting approach due to the low sample size (n = 10 individuals) and hence the high likelihood of overfitting (Anderson and Burnham 2002; Harrison et al. 2018). Pearson's product-moment correlations were used to estimate the covariance between (a) average daily display/sneak frequency and (b) body area, emergence time, colour area and colour diversity. We used the sequential

Bonferroni procedure (Rice 1989) to correct for multiple comparisons. Emergence times were log transformed to comply with the assumption of normality. Following Biro (2012) and Beckmann and Biro (2013), we used mixed-model best linear unbiased predictors (BLUPs) to estimate individual values for display and sneak frequency. Data were analysed using Statistica v7 and the R programming language (v3.5.2; R Development Core Team 2017).

Data availability

All data generated or analysed during this study are included in this published article and its supplementary information files.

Results

Diel schedules of sexual activity

Overall, the daily frequency of both displays and sneaks varied significantly across observation hours (Tables 1 and 2) and tended to be higher in the morning compared to midday (Figs. 2 and 3). For displays, there was a significant hour × treatment interaction (treated further below); hence, we investigated diel variation further via separate GLMMs for each light environment (full detail is provided in supplementary online Table S1). These models indicated significant hourly variation in daily display frequency under both the normal light regime ($F_{6.67,\ 265} = 8.02$, $P < 0.001$) and the prolonged dawn regime ($F_{6,\ 6.67} = 8.02$, $P < 0.001$).

As predicted, the daily frequency of male displays under the normal light regime declined sharply from early morning onwards (Fig. 2a). Post hoc testing revealed a difference only between 0800 and all other hours. The prolonged dawn regime, however, engendered a longer period of morning display and a more gradual decline into the afternoon (Fig. 2b). The lowest average daily display frequency under each regime moreover aligned with the hour of highest light intensity (i.e. 1200 for the normal regime, 1400 for the prolonged dawn treatment). These results support the prediction that prolonging the period of dawn-like lighting within the same circadian cycle prompts a more extended period of high-display activity.

It is possible that habituation could explain some differences between the normal and prolonged dawn regimes. Multiple groups with random treatment order would be required to address this directly. However, we included date (the number of days following the beginning of the experiment) in the model as a covariate to account for this statistically.

Table 2 GLMM results for the analysis of male daily sneak frequency. This analysis used a zero-inflated Poisson distribution. Significant effects are in italic type

Model/term	Effect	Estimate	SE	*z*	*P*
Zero-inflation model	Intercept	0.102	0.105	0.976	0.329
Conditional model	*Intercept*	*3.75*	*1.25*	*2.99*	*< 0.005*
Fish	Random	− 0.255	0.142	− 1.80	0.0725
Hour	*Fixed*	*− 0.328*	*0.114*	*− 2.87*	*< 0.005*
Treatment	Fixed	− 1.25	1.45	− 0.861	0.389
Fish*hour	Random	0.0251	0.0129	1.95	0.0512
Fish*treatment	Random	0.156	0.165	0.942	0.346
Hour*treatment	Fixed	0.220	0.133	1.66	0.0968
Fish*hour*treatment	Random	− 0.0166	0.0152	− 1.09	0.274
Date	Covariate	− 0.0262	0.0185	− 1.42	0.156

Table 1 GLMM results for the analysis of male daily display frequency

Model term	Effect	df	MS	Den. syn. error df	Den. syn. error MS	*F*	*P*
Intercept	Fixed	1	0.231	441	14.9	0.016	0.901
Fish	Random	9	118	9.72	98.2	1.20	0.388
Hour	*Fixed*	*6*	*201*	*54.8*	*12.5*	*16.1*	*< 0.001*
Treatment	Fixed	1	0.432	92.0	18.6	0.023	0.879
Fish*hour	Random	54	12.4	54.0	8.58	1.45	0.0869
*Fish*treatment*	*Random*	*9*	*95.8*	*59.8*	*8.74*	*11.0*	*< 0.001*
*Hour*treatment*	*Fixed*	*6*	*54.2*	*55.2*	*8.61*	*6.29*	*< 0.001*
Fish*hour*treatment	Random	54	8.58	545	13.8	0.620	0.985
Date	*Fixed*	*1*	*242*	*545*	*13.8*	*17.5*	*< 0.001*
Error		545	13.8				

Significant effects including fish (individual ID), hour (0800 to 1430) and treatment regime (natural and manipulated light cycles) are in italic type. The table contains two columns, Den. syn. (denominator synthesis) error df and Den. syn. error MS, indicating the appropriate error term to use in tests of significance for each effect and the degrees of freedom associated with that term. Reported *F* and *p* values are based on those denominator syntheses mean squares. Significant effects are italic.

*Indicates an interaction

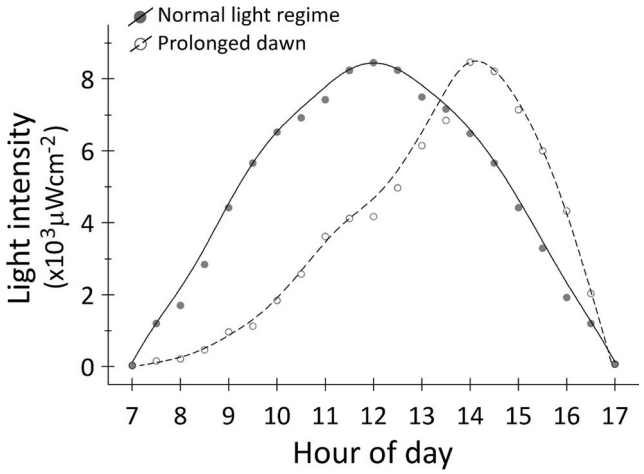

Fig. 1 Diel regimes of tank illumination as established for each of the two treatment light environments. Fish were housed under each light regime for 2 weeks prior to observing sexual activity

Individual variation

The overall GLMM analysis of male daily display frequency indicated no main effect of individual but a significant individual × treatment interaction. Separate GLMMs revealed significant variation among individuals under both the normal light regime ($F_{9,\ 69.3} = 26.4$, $P < 0.001$) and the prolonged dawn regime ($F_{9,\ 54.7} = 2.18$, $P < 0.05$; Table S1). There was no significant individual × hour interaction in either case. Hence, although males displayed at different daily frequencies, there was no support for varied diel patterns of display within each light treatment. Interestingly, the significant individual × treatment interaction (Fig. 4) revealed that males did not rank in the same order for daily display frequency across the two light regimes. That is, relatively high-displaying males under a normal light regime did not achieve this status under prolonged dawn conditions. In contrast to daily display frequency, there was no evidence for main or interactive effects of individual identity upon the daily frequency of sneaking (Table 3).

Relationships with broader phenotypic traits

Given that males ranked differently for daily display frequency across treatment light regimes (Fig. 4), we explored the relatedness between this trait and broader phenotypic traits separately for each treatment. Intriguingly, even despite the low statistical power, the data indicate strong and significant links between individual daily display frequency and both colour diversity (C_D) and emergence time, but only under the prolonged dawn regime (Table 3). Here, highly displaying males possessed more diverse ornamental phenotypes and daily display frequency correlated positively with latency to emerge in the emergence assay. Individual daily sneak frequency was not significantly related to any of the studied phenotypic characters (Table 3). Once again, differences in habituation between treatments may help explain this treatment effect.

Discussion

Ecological trade-offs between predation risk and resource availability can shape animal behaviour, leading to shifts in the frequency, time and habitat of which individuals choose to behave (Berger and Gotthard 2008). For example, in guppies, variation in predation risk leads to many plastic changes—as measured at the population level—including temporal shifts in the intensity of display behaviour versus sneak copulation attempts (Godin 1995), modified foraging behaviour (Fraser et al. 2004) and changes in foraging rate, spatial habitat use and shoaling behaviour (Botham, et al. 2006). Much less is,

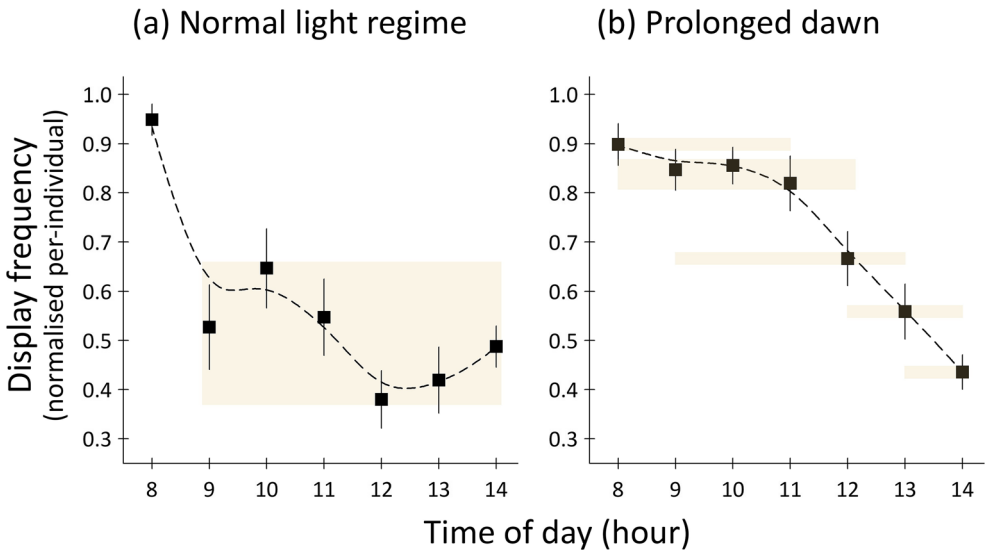

Fig. 2 **a**, **b** Diel patterns of male displays under each treatment light environment. The halftone horizontal bars in each panel indicate unique hourly groupings that did not differ (at $p < 0.05$) in post hoc contrasts according to Tukey's honest significant difference. The dependent variable was normalised for each individual to remove variance in each male's daily display frequency. Means are indicated ± 1 SE

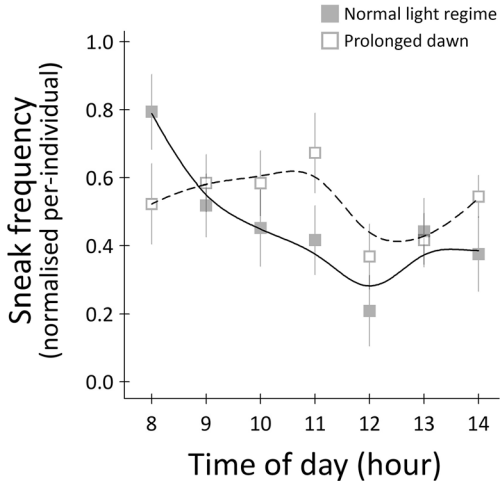

Fig. 3 Diel patterns of male sneaks under each treatment light environment. The dependent variable was normalised for each individual to remove variance in each male's daily sneak frequency. Means are indicated ±1 SE

however, known about how the consequences of opposing selective pressures are expressed at the level of individuals, which is a salient question given that male guppies vary in important traits such as size, colouration and behavioural tendencies. Our population-level analysis indicated not only that feral Australian guppies conform to a similar diel courtship schedule as their native Trinidadian counterparts but also that this schedule appears to be mediated similarly via changes in ambient light intensity. As discussed below, this may indicate evolutionary conservatism in guppy behaviour and/or convergent ecological circumstances, or alternatively that predation risk has been overstated as a driver of such patterns. At the individual level, we found that despite a lack of detectable

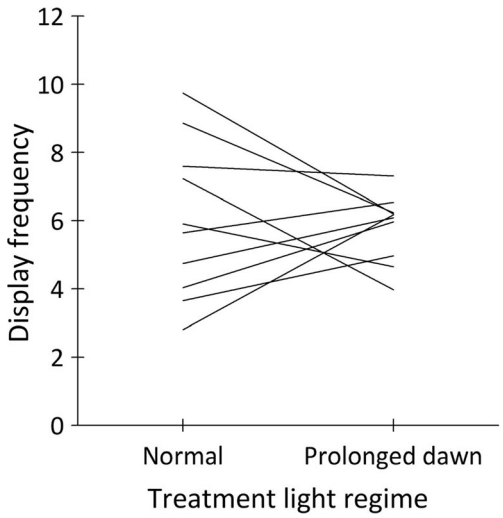

Fig. 4 The interaction between individual daily display frequency and treatment light environment. Each line traces an individual's mean daily display frequency (per-5 min observation interval) across the two environments. Means were estimated as least-squares adjusted values derived from the GLMM in Table 1

variation in diel scheduling, males varied in their overall frequency of courtship display behaviour. Related to this, our data point to intriguing relationships between display frequency, ornamentation and a non-sexual measure of risk taking.

As predicted, daily display frequency was inversely related to light intensity under both experimental light regimes. This implicates light regime, rather than time of day, as the main proximate driver of changes in display frequency. The timing and control of this behaviour are therefore very similar to those reported for native Trinidadian guppies (Endler 1987; Archard et al., 2009). Strictly, when we refer to daily patterns in our population, we can refer only to our observation window (0700–1430), which did not include the final 2.5 h of light. However, given the causal link between light and display in this population, we feel that extrapolating these results to daily behaviour is reasonable. Previously, the cause of the diel display pattern was primarily linked to predation, and to the activity of a single species, *C. frenata* (Endler 1987). Subsequently, the same diel pattern was discovered in low-predation populations where *C. frenata* is not present (Archard et al. 2009). We extend this finding to feral Australian guppies sourced from a population living under a completely different suite of predators than Trinidadian guppies and transplanted into a lab environment with no predators.

There are many possible reasons for why guppies exhibit this diel pattern of display across differing ecological contexts. Australian predators may be functionally similar to Trinidadian predators by being more active under higher light. Alligator Creek is home to many different predators, and these vary throughout the wet and dry seasons. The marbled eel (*Anguila* sp.) and jungle perch (*Kuhlia rupestris*) are thought to be guppies' main predators in the area (Lindholm et al. 2014), but the site is also home to spangled perch (*Leiopotherapon unicolour*), various eel species (*Anguila* sp.), and the banded grunter (*Amniataba percoides*). Little is known about the feeding patterns of these predators except that the *Anguila* sp. are likely to be nocturnal. However, even if these predators are more active in the mornings and afternoons, low-light conditions may be inherently safer due to the reduced transmission of guppy colour signals under these conditions (Endler 1987). It is also possible that factors other than predator community composition (or predation risk per se) drive the relationship between light levels and display frequency. Female sexual receptivity and/or responsiveness to male display may vary throughout the day, or itself be sensitive to variation in light level. Females are known to drive male guppy display behaviour in other situations (Cole and Endler 2016; see below for discussion). The accessibility or receptivity of females may of course itself be shaped by predation risk. Indeed, female perception of predation risk drives changes in the sexual behaviour of males even if the males themselves are unaware of such risks (Evans et al. 2002).

Table 3 Univariate relationships (Pearson's r values) between individual male traits and daily display/sneak frequency. Daily display frequency was analysed separately for each light environment due to the presence of individual × environment interaction (Fig. 3)

	Daily display frequency		Daily sneak frequency
	Environment 1 (normal regime)	Environment 2 (prolonged dawn)	Environments 1 and 2
Body size (lateral area)	0.470	0.265	0.438
Colour area (C_A)	0.005	0.681*	− 0.112
Colour diversity (C_D)	0.153	*0.939**	0.262
Latency to emergence	0.360	*0.831**	− 0.202

Significant relationships ($p < 0.05$) are marked with an asterisk, while those remaining significant after sequential Bonferroni correction (Rice 1989) are in italic type

Investigating the diel patterns of female receptivity to courtship and mating would be fruitful. This means that the ultimate causality of predation upon male display effort will prove difficult to isolate.

Our findings contrast with those of Kelley et al. (2013), who found no overall effect of changing light intensity on sexual behaviour in guppies from Alligator Creek. However, their study population was 12th generation lab reared (in contrast to this study's wild-caught population) and had not experienced predation or diel light schedules. The difference in findings may therefore indicate the loss or modification of display schedules due to captive breeding, that is, an effect akin to domestication. Alternatively, this could suggest a learnt or 'environmental' cause of the behaviour due to, for example, experiencing predators, though see Reynolds et al. (1993) who found an effect of light on third-generation laboratory-bred guppies.

Sneak copulation attempts varied according to time of day, though the relationship between light and sneak attempts was not clear. Sneak copulation attempts appear less visually conspicuous compared to full displays and may allow males to increase their number of copulations while mitigating predation risk (Endler 1987). However, based on previous work on guppies, it was difficult to predict how sneak behaviour should vary under the changing environments of this study. Endler (1987) and Reynolds et al. (1993) found no effect of light environment on the number of sneaks, whereas Archard et al. (2009) found that males attempted more sneak copulations under higher light levels. Evans et al. (2002) found that changes in female receptivity led to males allocating more time into attempting sneak copulations over displays. Male guppies have also been found to vary their frequency of sneak attempts according to ambient light spectra (Gamble et al. 2003). Kelley et al. (2013) found no population effect of light intensity on sneak behaviour but found individual-by-light environment interaction effects on sneak behaviour. Although we found that sneak behaviour varied according to time of day, the absence of any hour-by-treatment interaction implies that light levels did not primarily drive this variation, supporting the findings of Kelley et al. (2013). However, individuals did not vary significantly in sneak attempts, nor were there any interaction effects between individual and lighting treatment. This is consistent with sneak behaviour as a less risky but more opportunistic means of seeking copulations.

Guppies have been previously shown to exhibit covariation between mating behaviour, sexual signalling behaviour and male morphology (Matthews et al. 1997; Archard et al. 2009). Our data suggest that this covariation can extend to non-sexual behaviours and potentially broader animal personality traits. Interestingly, we observed strong correlations between male daily display frequency and colour diversity and emergence behaviour in fish under the prolonged dawn regime but not under the normal regime. For colour, males that displayed more in the prolonged dawn environment had higher colour diversity. Display frequency in the prolonged dawn environment was significant before but not after Bonferroni correction. Previously, Nicoletto (1993) found a positive relationship between orange colouration and display frequency. However, visual signals represent the sum of multiple components, so understanding how colour diversity and total coverage effect behaviour is important. Guppies that displayed more in the 'extended dawn' environment also had longer emergence times. Longer emergence may infer a shyer individual behavioural type, and therefore that bolder individuals may in fact display at a lower frequency. However, emergence alone cannot measure personality and thus a wider array of behavioural assays is required to confirm this. Despite the abundance of research investigating guppy sexual behaviour, few prior studies have investigated links between display frequency and personality.

Why these traits correlated to daily display frequencies in environment two and not one is difficult to understand, as we did not expect an individual-by-treatment interaction. Reynolds (1993) found that a change in light intensity reversed a correlation between size and display frequency; large males displayed more and were preferred by females at low light levels while small males displayed more (with no difference in female preference) at high light levels. It is possible that average differences in light levels between the two

treatments, particularly in the 0700–1430 observation window, may lead to such an interaction. However, we found no evidence of a light/dark interaction within treatments. Because our population came from the wild, but our treatments were sequential, it is also possible that differences in habituation explain the different results between light environments. Although we did our best to account for this statistically, this concern would be best approached with a different experimental design that uses multiple groups and randomised treatment order. However, because of the close relationship between light intensity and display frequency, we believe it is unlikely that habituation rather than the manipulation of light regime explains the main results of this study. While these findings are limited, we suggest that the relationship between display frequency and personality should be investigated more thoroughly.

We found that individuals varied in their overall daily display frequency but did not differ in their diel patterns of that behaviour. The latter is somewhat surprising because predator activity and interactions between ambient light and male colour signals are thought to drive the diel pattern of displays (Endler 1987; Archard et al. 2009) and there is substantial individual variation in colouration and predator tolerance in male guppies (Dugatkin 1992; Endler and Houde 1995; Godin and Dugatkin 1996). If male courtship levels are driven by something outside of these factors, such as female receptivity, then this may explain why variation in diel schedules should be subtle. Female receptivity has been found to strongly drive changes in male display behaviour under different light spectra (Cole and Endler 2016). Unfortunately, behavioural signs of female receptivity are observed at low frequencies in the wild. However, female swimming proximity to the male, one indicator of female receptivity, was not found to vary significantly under different light intensity treatments (Archard et al. 2009). Research into individual differences in different contexts would be fruitful to investigate this complexity. The growth of the animal personality field has led to the investigation of many behaviours within any given context. However, understanding how individuals adjust their behaviour over environmental gradients, both temporal and spatial, is critically important for understanding animal behaviour in the real world.

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Compliance with ethical standards

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

Ethical approval All procedures performed in studies involving animals were approved by and in accordance with the guidelines outlined by the Macquarie University Animal Ethics committee (Approval No. ARA 2017/035-12).

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References

Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. J Wildl Manag 66:912–918. https://doi.org/10.1111/10.2307/3803155

Archard GA, Cuthill IC, Partridge JC (2009) Light environment and mating behavior in Trinidadian guppies (*Poecilia reticulata*). Behav Ecol Sociobiol 64:169–182. https://doi.org/10.1007/s00265-009-0834-2

Beckmann C, Biro PA (2013) On the validity of a single (boldness) assay in personality research. Ethology 119:937–947. https://doi.org/10.1111/eth.12137

Berger D, Gotthard K (2008) Time stress, predation risk and diurnal–nocturnal foraging trade-offs in larval prey. Behav Ecol Sociobiol 62:1655–1663. https://doi.org/10.1007/s00265-008-0594-4

Biro PA (2012) Do rapid assays predict repeatability in labile (behavioural) traits? Anim Behav 83:1295–1300. https://doi.org/10.1016/j.anbehav.2012.01.036

Bischoff RJ, Gould JL, Rubenstein DI (1985) Tail size and female choice in the guppy (*Poecilia reticulata*). Behav Ecol Sociobiol 17:253–255. https://doi.org/10.1007/BF00300143

Botham MS, Kerfoot CJ, Louca V, Krause J (2006) The effects of different predator species on antipredator behavior in the Trinidadian guppy, *Poecilia reticulata*. Naturwissenschaften 93:431–439. https://doi.org/10.1007/s00114-006-0131-0

Brooks R, Endler JA (2001) Female guppies agree to differ: phenotypic and genetic variation in mate-choice behaviour and the consequences for sexual selection. Evolution 55:1644–1655. https://doi.org/10.1111/j.0014-3820.2001.tb00684.x

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Brown C, Jones F, Braithwaite VA (2007) Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcopi*. J Fish Biol 71:1590–1601. https://doi.org/10.1111/j.1095-8649.2007.01627.x

Chapman BB, Hulthén K, Blomqvist DR, Hansson LA, Nilsson JA, Brodersen J, Anders Niolsson P, Skov C, Brönmark C (2011) To boldly go: individual differences in boldness influence migratory tendency. Ecol Lett 14:871–876. https://doi.org/10.1111/j.1461-0248.2011.01648.x

Cole GL, Endler JA (2016) Male courtship decisions are influenced by light environment and female receptivity. Proc R Soc B 283:20160861. https://doi.org/10.1098/rspb.2016.0861

Deacon AE, Ramnarine IW, Magurran AE (2011) How reproductive ecology contributes to the spread of a globally invasive fish. PLoS One 6:e24416. https://doi.org/10.1371/journal.pone.0024416

Dosen LD, Montgomerie R (2004) Female size influences mate preferences of male guppies. Ethology 110:245–255. https://doi.org/10.1111/j.1439-0310.2004.00965.x

Dugatkin LA (1992) Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia reticulata*). Behav Ecol 3:124–127. https://doi.org/10.1093/beheco/3.2.124

Endler JA (1978) A predator's view of animal color patterns. In: Hecht MK, Steere WC, Wallace B (eds) Evolutionary biology. Springer, Boston, pp 319–364

Endler JA (1980) Natural selection on color patterns in *Poecilia reticulata*. Evolution 34(1):76–91

Endler JA (1987) Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Anim Behav 35:1376–1385. https://doi.org/10.1016/S0003-3472(87)80010-6

Endler JA (1990) On the measurement and classification of colour in studies of animal colour patterns. Biol J Linn Soc 41:315–352

Endler JA, Houde AE (1995) Geographic variation in female preferences for male traits in *Poecilia reticulata*. Evolution 49:456–468. https://doi.org/10.2307/2410270

Evans JP, Kelley JL (2008) Implications of multiple mating for offspring relatedness and shoaling behaviour in juvenile guppies. Biol Lett 4:623–626. https://doi.org/10.1098/rsbl.2008.0423

Evans JP, Kelley JL, Ramnarine IW, Pilastro A (2002) Female behaviour mediates male courtship under predation risk in the guppy (*Poecilia reticulata*). Behav Ecol 52:496–502. https://doi.org/10.1007/s00265-002-0535-6

Fraser DF, Gilliam JF, Akkara JT, Albanese BW, Snider SB (2004) Night feeding by guppies under predator release: effects on growth and daytime courtship. Ecology 85:312–319. https://doi.org/10.1890/03-3023

Gamble S, Lindholm AK, Endler JA, Brooks R (2003) Environmental variation and the maintenance of polymorphism: the effect of ambient light spectrum on mating behaviour and sexual selection in guppies. Ecol Lett 6:463–472. https://doi.org/10.1046/j.1461-0248.2003.00449.x

Godin J-GJ (1995) Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). Oecologia 103:224–229. https://doi.org/10.1007/bf00329084

Godin J-GJ, Dugatkin LA (1995) Variability and repeatability of female mating preference in the guppy. Anim Behav 49:1427-1433. https://doi.org/10.1016/0003-3472(95)90063-2

Godin J-GJ, Dugatkin LA (1996) Female mating preference for bold males in the guppy, *Poecilia reticulata*. P Natl Acad Sci USA 93:10262–10267. https://doi.org/10.1073/pnas.93.19.10262

Harris S, Ramnarine IW, Smith HG, Pettersson LB (2010) Picking personalities apart: estimating the influence of predation, sex and body size on boldness in the guppy *Poecilia reticulata*. Oikos 119:1711–1718. https://doi.org/10.1111/j.1600-0706.2010.18028.x

Harrison XA, Donalseon L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CE, Robinson BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6:e4794. https://doi.org/10.7717/peerj.4794

Heathcote RJP, Darden SK, Franks DW, Ramnarine IW, Croft DP (2017) Fear of predation drives stable and differentiated social relationships in guppies. Sci Rep 7:41679. https://doi.org/10.1038/srep41679

Hoffmann T (2017). SunCalc, https://www.suncalc.org/

Houde AE (1988) The effects of female choice and male-male competition on the mating success of male guppies. Anim Behav 36:888–896. https://doi.org/10.1016/S0003-3472(88)80171-4

Houde AE (1994) Effect of artificial selection on male colour patterns on mating preference of female guppies. Proc R Soc Lond B 256:125–130. https://doi.org/10.1098/rspb.1994.0059

Houde AE (1997) Sex, color, and mate choice in guppies. Princeton University Press, Princeton

Huntingford FA (1976) The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. Anim Behav 24:245–260. https://doi.org/10.1016/S0003-3472(76)80034-6

Johansson J, Turesson H, Persson A (2004) Active selection for large guppies, *Poecilia reticulata*, by the pike cichlid, *Crenicichla saxatilis*. Oikos 105:595–605. https://doi.org/10.1111/j.0030-1299.2004.12938.x

Karino K, Kamada N (2009) Plasticity in courtship and sneaking behaviors depending on tail length in the male guppy, *Poecilia reticulata*. Ichthyol Res 56:253–259. https://doi.org/10.1007/s10228-008-0093-7

Kelley JL, Phillips SC, Evans JP (2013) Individual consistency in exploratory behaviour and mating tactics in male guppies. Naturwissenschaften 100:965–974. https://doi.org/10.1007/s00114-013-1097-3

Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall J, Whiting MJ (2015) An Integrative Framework for the Appraisal of Coloration in Nature. The American Naturalist 185 (6):705–724

Kemp DJ, Reznick DN, Grether GF, Endler JA (2009) Predicting the direction of ornament evolution in Trinidadian guppies *Poecilia reticulata*. Proc R Soc Lond B 276:4335–4343. https://doi.org/10.1098/rspb.2009.1226

Kerman K, Sieving KE, Mary CS, Avery ML (2016) Evaluation of boldness assays and associated behavioral measures in a social parrot, monk parakeet (*Myiopsitta monachus*). Behaviour 153:1817–1838

Kortet R, Hendrick A (2007) A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. Biol J Linn Soc 91:475–482. https://doi.org/10.1111/j.1095-8312.2007.00812.x

Kotrschal A, Lievens EJ, Dahlbom J, Bundsen A, Semenova S, Sundvik M, Maklakov AA, Winberg S, Panula P, Kolm N (2014) Artificial selection on relative brain size reveals a positive genetic correlation between brain size and proactive personality in the guppy. Evolution 68:1139–1149. https://doi.org/10.1111/evo.12341

Lindholm AK, Breden F, Alexander HJ, Chan W-K, Thakurta SG, Brooks RC (2005) Invasion success and genetic diversity of introduced populations of guppies *Poecilia reticulata* in Australia. Mol Ecol 14:3671–3682. https://doi.org/10.1111/j.1365-294X.2005.02697.x

Lindholm AK, Head ML, Brooks RC, Rollins LA, Ingleby FC, Zajitschek SRK (2014) Causes of male sexual trait divergence in introduced populations of guppies. J Evol Biol 27:437–448. https://doi.org/10.1111/jeb.12313

Magellan K, Pettersson LB, Magurran AE (2005) Quantifying male attractiveness and mating behaviour through phenotypic size manipulation in the Trinidadian guppy, *Poecilia reticulata*. Behav Ecol Sociobiol 58:366–374. https://doi.org/10.1007/s00265-005-0950-6

Magurran AE, Seghers BH (1990) Risk sensitive courtship in the guppy (*Poecilia Reticulata*). Behaviour 112:194–201. https://doi.org/10.1163/156853990X00194

Mariette M, Kelley JL, Brooks R, Evans JP (2006) The effects of inbreeding on male courtship behaviour and coloration in guppies. Ethology 112:807–814. https://doi.org/10.1111/j.1439-0310.2006.01236.x

Matthews IM, Evans JP, Magurran AE (1997) Male display rate reveals ejaculate characteristics in the Trinidadian guppy, *Poecilia reticulata*. Proc R Soc Lond B 264:695–700. https://doi.org/10.1098/rspb.1997.0099

Millar NP, Reznick DN, Kinnison MT, Hendry AP (2006) Disentangling the selective factors that act on male colour in wild guppies. Oikos 113:1–12. https://doi.org/10.1111/j.0030-1299.2006.14038.x

Nicoletto PF (1993) Female sexual response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. Anim Behav 46:441–450. https://doi.org/10.1006/anbe.1993.1213

O'Neill SJ, Williamson JE, Tosetto L, Brown C (2018) Effects of acclimatisation on behavioural repeatability in two behaviour assays of the guppy *Poecilia reticulata*. Behav Ecol Sociobiol 72:166–111. https://doi.org/10.1007/s00265-018-2582-7

Pilastro A, Bisazza A (1999) Insemination efficiency of two alternative male mating tactics in the guppy *Poecilia reticulata*. Proc R Soc Lond B 266:1887–1891. https://doi.org/10.1098/rspb.1999.0862

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Austria http://www.R-project.org

R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org

Reynolds JD, Gross MD, Coombs MJ (1993) Environmental conditions and male morphology determine alternative mating behaviour in Trinidadian guppies. Anim Behav 45:145–152. https://doi.org/10.1006/anbe.1993.1013

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225. https://doi.org/10.1111/j.1558-5646.1989.tb04220.x

Rodd HF, Sokolowski MB (1995) Complex origins of variation in the sexual behaviour of male Trinidadian guppies, *Poecilia reticulata*: interactions between social environment, heredity, body size and age. Anim Behav 49:1139–1159. https://doi.org/10.1006/anbe.1995.0149

Satterthwaite FE (1946) An approximate distribution of estimates of variance components. Biometrics 2(6):110–114

Sih A, Bell AM, Johnson JC, Ziemba RE (2004) Behavioral syndromes: an integrative overview. Q Rev Biol 79:241–277. https://doi.org/10.1086/422893

Sih A, Cote J, Evans M, Fogarty S, Pruitt J (2012) Ecological implications of behavioural syndromes. Ecol Lett 15:278–289. https://doi.org/10.1111/j.1461-0248.2011.01731.x

Stapley J, Keogh JS (2005) Behavioral syndromes influence mating systems: floater pairs of a lizard have heavier offspring. Behav Ecol 16:514–520. https://doi.org/10.1093/beheco/ari019

Vuong QH (1989) Likelihood ratio tests for model selection and non-nested hypotheses. Econometrica 307–333

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