

# Testing for a whole-organism trade-off between natural and sexual selection: are the male guppies preferred by females more likely to be eaten by predators?

José Jonathas P.R. de Lira, Felipe Peréz-Jvostov, Kiyoko M. Gotanda\*, Sian Kou-Giesbrecht<sup>#</sup>, Sarah K. Pease<sup>^</sup>, Marlee Jackson, Shaffiq Jersch and Andrew P. Hendry

*Department of Biology and Redpath Museum, McGill University, Montreal, Quebec, Canada*

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## ABSTRACT

**Background:** Trade-offs between natural and sexual selection have major consequences for the evolution of traits subject to both forces. However, such a trade-off might not be easily detected given that both natural and sexual selection operate in a multi-trait – rather than in a single-trait – manner.

**Organism:** The Trinidadian guppy, *Poecilia reticulata* (Osteichthyes).

**Hypothesis:** Males preferred by females are more susceptible to predation.

**Aim:** Develop and apply a whole-organism, performance-based test for a trade-off between natural and sexual selection.

**Methods:** We conducted three different experiments involving pairs of males in female choice trials followed by the same pairs of males in predation trials. The hypothesis was tested with chi-square contingency table analyses for each experiment separately and for all data combined.

**Results:** Males preferred by females were not more likely to be eaten by a predator.

**Conclusion:** The whole-organism, performance-based trade-off is absent, very weak, or context-dependent, making it difficult to detect in experiments.

*Keywords:* mate choice, performance, *Poecilia reticulata*, predation.

## INTRODUCTION

Traits favoured by sexual selection, especially through mate choice, are classically assumed to be disfavoured by natural selection owing to predation, parasitism, and energy costs

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Correspondence: J.J.P.R. de Lira, Department of Biology and Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec H3A 2K6, Canada. email: lirajjpr@gmail.com

\**Present address:* Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.

<sup>#</sup>*Present address:* Department of Ecology, Evolution, and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, USA.

<sup>^</sup>*Present address:* Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, VA 23062, USA.

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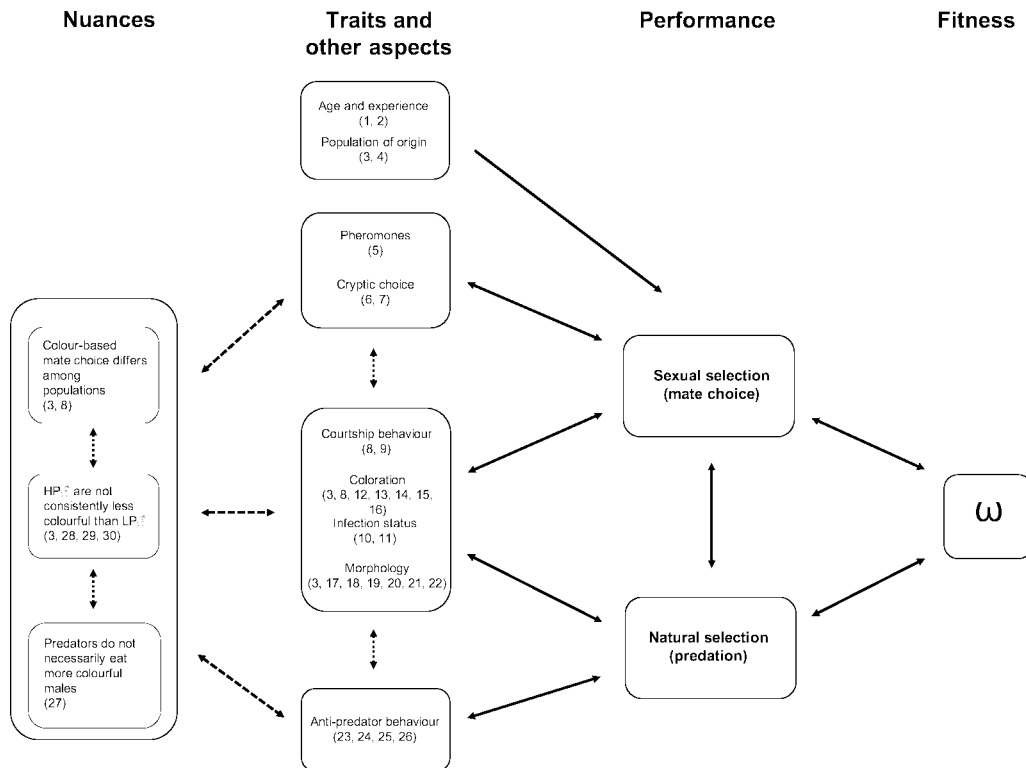
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(Darwin, 1871; Endler, 1980; Andersson, 1994; Zuk and Kolluru, 1998; Kotiaho, 2001). This expectation has been borne out in a number of specific empirical systems (Zuk and Kolluru, 1998; Rosenthal *et al.*, 2001; Hunt *et al.*, 2004; Hurtado-Gonzales *et al.*, 2010; Hernandez-Jimenez and Rios-Cardenas, 2012; Heinen-Kay *et al.*, 2015; Johnson and Candolin, 2017), yet meta-analyses seeking broad support for such trade-offs are often unsuccessful. For example, males with larger ornaments had, on average, higher survival in a meta-analysis of 122 estimates from 60 studies of 40 species (Jennions *et al.*, 2001). Additionally, Kingsolver and Diamond (2011) found that selection differentials and gradients based on mating success were not correlated with those based on viability. Even acknowledging the limitations of such meta-analyses (Parker, 2013), it is clear that trade-offs between sexual and natural selection are not a universal finding across traits and systems.

We suggest that one reason for the frequent failure to document trade-offs between natural and sexual selection could be that nearly all studies focus on individual traits, whereas natural and sexual selection reflect a multivariate combination of large suites of traits (Brooks *et al.*, 2005; Prokop and Drobniak, 2016). Such suites of traits combine in complex ways to generate functions that determine the ability of an organism to perform an ecologically relevant task, i.e. ‘performance’ (Arnold, 1983; Lailvaux and Irschick, 2006; Irschick *et al.*, 2008). Hence, selection should operate directly on performance and only indirectly on the individual component traits that influence performance (Arnold, 1983; Lailvaux and Irschick, 2006). For instance, females might choose mates based not just on their colour *or* behaviour *or* size *or* speed *or* sound *or* smell; instead, they might choose mates based on their colour *and* behaviour *and* size *and* speed *and* sound *and* smell (Brooks and Endler, 2001b; Blows *et al.*, 2003; Roberts *et al.*, 2007). In such cases, sexual selection based on mate choice should act on a multivariate combination of these mating signals. Reciprocally, susceptibility to predation (or, more generally, mortality) is likely influenced by size *and* speed *and* vision *and* behaviour *and* sound *and* smell (Roberts *et al.*, 2007; Cooper and Blumstein, 2015), such that only in combination will these traits predict survival.

In such highly multivariate contexts for both natural and sexual selection, we would not necessarily expect a trade-off for any one (or few) of the traits, but rather a trade-off integrated across overall multivariate trait space or, more directly, a trade-off in performance itself. Thus, one approach to exploring trade-offs might be to measure as many traits as possible and then to analyse their contributions to natural and sexual selection in a multivariate framework (Brooks and Coullidge, 1999; Blows *et al.*, 2003; Hunt *et al.*, 2005; Bentsen *et al.*, 2006; Reding and Cummings, 2017). However, this approach is often impractical, and inevitably incomplete, because potentially important traits could include many known and unknown aspects of morphology *and* behaviour *and* physiology *and* life history. We therefore propose a re-emphasis on the core question – the expectation of a whole-organism performance trade-off between natural and sexual selection. An exemplar of this focus would be a test to determine whether the specific males that are preferred by females are more likely to be eaten by a predator, generating a whole-organism, performance-based test for whether sexual selection trades off with natural selection.

We test for this whole-organism trade-off between natural and sexual selection in experiments with the Trinidadian guppy (*Poecilia reticulata* Peters, 1859). Guppies are a logical focus for this work because previous trait-based approaches have suggested trade-offs between male mating success and male viability (Fig. 1). However, the outcomes of previous studies are highly nuanced, and several factors are known to influence either mating success or susceptibility to predation in guppies. All of these traits, then, influence the performance of males in terms of mating success and/or survival, and ultimately determine their fitness



**Fig. 1.** Diagram demonstrating the role played by male traits and other aspects in the natural and sexual selection systems of guppies. These traits directly or indirectly determine the performance of male guppies in terms of mate choice and survival, and, by doing so, are influenced by sexual and natural selection in turn. HP♂ indicates males from environments with high risk of predation; LP♂ indicates males from environments with low risk of predation. Double-headed arrows indicate bidirectional influence. Numbers indicate studies: 1, Rosenqvist and Houde (1997); 2, Kodric-Brown and Nicoletto (2001); 3, Endler and Houde (1995); 4, Schwartz *et al.* (2010); 5, Shohet and Watt (2004); 6, Evans *et al.* (2003); 7, Pilastro *et al.* (2004); 8, Houde (1997); 9, Godin and Davis (1995); 10, Kolluru *et al.* (2009); 11, Kennedy *et al.* (1987); 12, Magurran (2005); 13, Endler (1995); 14, Olendorf *et al.* (2006); 15, Weese *et al.* (2010); 16, Gordon *et al.* (2015); 17, Reynolds and Gross (1992); 18, Brooks and Caithness (1995); 19, Endler (1980); 20, Johansson *et al.* (2004); 21, Endler (1978); 22, Hendry *et al.* (2006); 23, Seghers (1974a); 24, Seghers (1974b); 25, Dugatkin (1992); 26, Heathcote *et al.* (2017); 27, Weese *et al.* (2011); 28, Karim *et al.* (2007); 29, Millar *et al.* (2006); 30, Gotanda *et al.* (2013).

(Fig. 1). Guppies therefore seem an appropriate system to test for a whole-organism trade-off between natural and sexual selection.

Our study design seeks to answer two simple questions: (1) when given a choice between two males, which one does a female guppy prefer – that is, male performance based on female choice; and (2) when those two males are exposed to a native predator (*Crenicichla* sp. Eigenmann, 1912), which male is eaten first – that is, male performance based on survival. We predict that, if the whole-organism performance trade-off between natural and

sexual selection is strong, the male preferred by the female should be more likely to be eaten first by the predator. We performed three different experiments that independently tested this prediction.

## METHODS AND MATERIALS

### Fish origin and maintenance

Guppies used in the experiments were either from a high predation locality in the Quare River in Trinidad, or were laboratory-reared, the latter being descendants of multiple generations of mixed wild-caught populations from Trinidad. The *Crenicichla* sp. used as predator was also wild-caught in the Quare River. All wild-caught fish were live-transported to McGill University where they were housed appropriately.

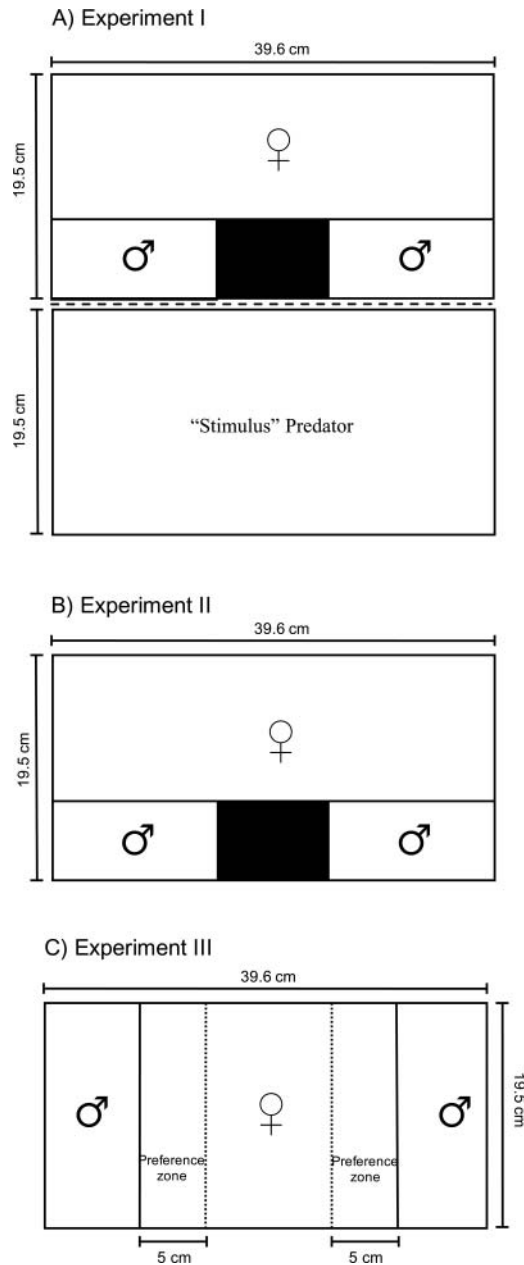
All fish were treated with Polyguard for bacterial and parasite infection before being used in the experiments. Guppies were fed daily brine shrimp or liver paste *ad libitum* (Experiments I and II) or brine shrimp only (Experiment III), while pike cichlids were fed daily bloodworms or live guppies. Both guppies and cichlids were not fed on the day they were used in a trial. All fish were maintained at a room temperature of 27°C and under a natural 12:12 hour (light:dark) photoperiod. All experiments were conducted at McGill University, Canada, under standardized conditions.

### General description of experiments

Although the specifics of the designs were different among experiments (Fig. 2), they all addressed the same focal question: whether a native predator, the pike cichlid *Crenicichla* sp., was more or less likely to prey upon the male guppy (in a given pair of males in a trial) that was previously preferred by a female guppy. In all three experiments, we implemented a dichotomous choice design for the female preference trials – males and females were acclimated in the tank for 10 minutes before a trial. Following the female preference trial, males were placed simultaneously into the predator tank. All males and females were used only once. In all cases, we used two predators, alternating which one was used in a given trial. Experiments were conducted in 2010 and 2011 (Experiment I), 2012 and 2013 (Experiment II), and 2015 (Experiment III).

### Differences between experiments and video analysis

Two weeks before the experiments, all guppies were separated by sex (in Experiment III, male guppies were also separated by colour, in such a way that colourful males were isolated from non-colourful males – colourful and non-colourful males were classified based on total amount of colour by visual inspection in the stock tanks). The selection of experimental males was made at random (Experiment I), based on the amount of orange, in such a way that in each trial one male had more orange than the other male in the pair (Experiment II), or based on the total amount of coloration, in such a way that the pair of males in each trial consisted of one colourful and one non-colourful male (Experiment III). A female was considered to be interacting with a male when she was within the ‘preference zone’ for that male, which was defined as one body length from that male’s compartment (Experiments I and II) or as a maximum distance of 5 cm from that male’s compartment



**Fig. 2.** Schematic representation of the experimental tanks ('mate choice tanks') used for the mate choice trials in the three experiments. Dashed line in (A) represents a removable opaque barrier. Dotted lines in (C) indicate the preference zone, within which the female was considered to be interacting with a male.

(Experiment III). In Experiment I, we used either a black or orange background (material immediately against the non-filming sides of the tank) in the mate choice and predator trials, but only a black background in Experiments II and III. In Experiment III, light bulbs and mesh were placed on top of each mate choice tank to simulate dawn and dusk, periods of the day in which guppies are most active and courtship occurs more often (Houde, 1997). Finally, in Experiment I, we exposed males and females to a ‘stimulus predator’ so that courtship would take place under threat of predation (Fig. 2). In Experiments I and III, if neither of the two males was eaten after an hour of observation, the trial was terminated; in Experiment III, however, we re-commenced the trials the following day.

The mate choice trials were recorded for 10 minutes (Experiments I and II) or 25 minutes (Experiment III) with a Canon Vixia HV40 high-definition camcorder. Males for which the females spent a greater proportion of time within their preference zone were classified as the ‘preferred male’, while males for which the females spent proportionately less time within their preference zone were classified as the ‘non-preferred male’. The time spent by a female in the preference zone was estimated using the software JWatcher 1.0. For this analysis, we used either a 5-minute segment from the middle of the 10-minute video (Experiments I and II), or the last 20 minutes from the 25-minute video (Experiment III).

### Statistical analysis

We computed the number of trials in which the preferred male was eaten or not eaten by the predator and constructed a  $2 \times 1$  contingency table. Then, for each experiment, we implemented a chi-square ( $\chi^2$ ) test to determine whether the males that were preferred by females were also more often eaten by the predator. These analyses were also applied to all experiments pooled together, yielding a much larger sample size than that obtained in any of the individual experiments. All analyses were performed using the R statistical software v. 3.2.5 (R Development Core Team, 2017).

## RESULTS

Males that were preferred by the female were not more often eaten by the predator in any of the experiments (Table 1). However, a trend was evident in the expected direction in two of the three experiments (Experiment I: 70% of the preferred males were eaten; Experiment II: 69% of the preferred males were eaten – Table 1, Fig. 3), suggesting that the lack of significance is driven by small sample sizes. There was also a lack of significance when pooling the data for all experiments (Table 1), mainly because Experiment III had the smallest difference between categories.

The magnitudes of the effects are considered to be medium in Experiments I and II (Table 1) (Cohen, 1988; Koricheva *et al.*, 2013), again suggesting that the lack of significance was driven by small sample sizes. We therefore also implemented a power analysis – using the R package ‘*pwr*’ (Champely, 2018) – to estimate the effect size that would result in a significant chi-square value given the sample size in each experiment: in all cases, it was extreme (Table 1). We also used a power analysis to estimate the sample size that would lead to a significant chi-square value given the actual effect size in each experiment: in all cases, the values were quite large (Table 1).

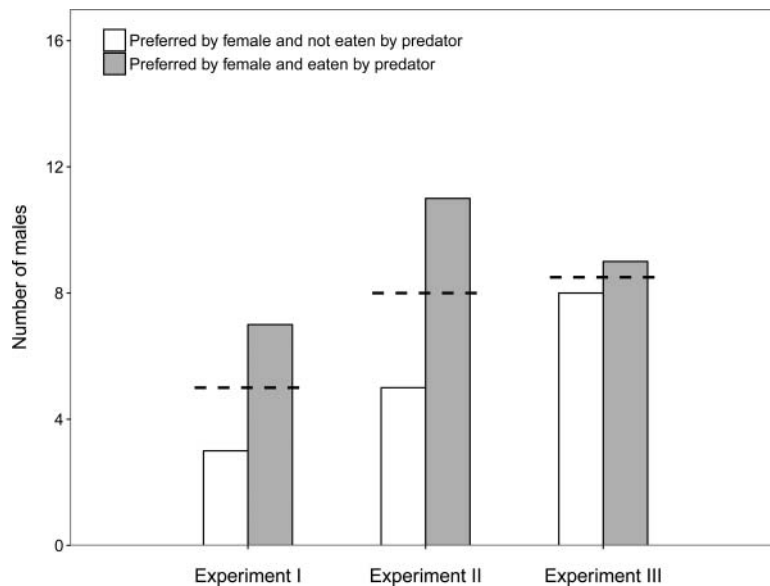
**Table 1.** Chi-square results for testing the probability that males preferred by females are more likely to be eaten by the predator in each of our three experiments, as well as pooled data across the three experiments. Measures of effect size are presented, as well as simulated effect sizes and sample sizes for which a chi-square test would be significant

	Exp. I	Exp. II	Exp. III	All combined
Males Preferred and eaten	7	11	9	27
Males Preferred and not eaten	3	5	8	16
$\chi^2$	1.6	2.25	0.059	2.8
$df$	1	1	1	1
$P$ -value	0.2	0.13	0.81	0.09
Effect size ( $w$ ) <sup>1</sup>	0.4	0.38	0.06	0.256
Significant effect size (simulated)	1.14	0.90	0.874	0.55
	(2.85× larger <sup>2</sup> )	(2.37× larger <sup>2</sup> )	(14.56× larger <sup>2</sup> )	(2.15× larger <sup>2</sup> )
Significant sample size (simulated)	81	90	3609	198
	(8.1× larger <sup>3</sup> )	(5.62× larger <sup>3</sup> )	(212.3× larger <sup>3</sup> )	(4.6× larger <sup>3</sup> )

<sup>1</sup> Effect size (ES) calculated as Cohen's  $w$  (Cohen, 1988; Champely, 2018).

<sup>2</sup> How much larger the simulated effect size is compared with the actual effect size at which the chi-square test would be significant.

<sup>3</sup> How much larger the simulated effect size is compared with the actual sample size at which the chi-square test would be significant.



**Fig. 3.** The number of male guppies that were preferred or not preferred by the female and eaten by the predator (*Crenicichla* sp.) in each of the three experiments. Dashed lines indicate 50% of the total number of trials in each experiment.

## DISCUSSION

The simplest conclusion to draw from our experiments is that a strong performance-based trade-off between natural and sexual selection was not evident: males preferred by females were not more likely to be eaten by the predator. We suggest that potential reasons for the lack of a trade-off fall into six categories: (1) context dependence; (2) variability of female mate choice; (3) inadequate measures of natural and sexual selection; (4) trade-offs not occurring at the whole-organism level; (5) trade-offs not occurring – or weak – at any level; (6) limitations of experimental design and apparatus. We consider each of these possibilities in turn.

First, female mate choice in guppies is highly context-dependent, depending for instance on mating history and environmental conditions (Houde, 1997; Magurran, 2005). Thus, we might not have hit on the specific set of conditions under which the trade-off between natural and sexual selection is most readily revealed. However, we did vary a number of conditions between experiments, such as perception of predation risk, origin of females, background colour, and so on, without finding a strong trade-off in any case.

Second, our results could have been influenced by the high variability in mate choice preferences among female guppies (Brooks and Endler, 2001a), a common phenomenon in many species (Jennions and Petrie, 1997). That is, even if predators base their selection on a particular combination of male traits, different females might select for different combinations of male traits.

Third, our surrogates for natural selection (short-term predator avoidance) or sexual selection (short-term dichotomous female choice) might not have been adequate. For instance, survival will be influenced by many other factors, including susceptibility to infection by pathogens (Zuk and Kolluru, 1998; van Oosterhout *et al.*, 2007), vulnerability to other predators (Magurran, 2005 and references therein), or competitive ability (Andersson, 1994; Hunt *et al.*, 2009). Similarly, male mating success will be influenced not only by female mate choice but also by male–male competition and ‘sneaky’ copulations (Houde, 1997; Magurran, 2005). These factors were not a part of our experiments, and yet they could be critical to trade-offs between natural and sexual selection. Future work on whole-organism trade-offs between natural and sexual selection ought ideally to examine the actual reproductive success of males in more realistic group contexts and the actual long-term survival of males faced with multiple realistic agents of selection.

Fourth, it is possible that the supposition we adopted to motivate our study – that whole-organism (as opposed to trait-specific) trade-offs are the best way to test the hypothesis – is misguided. For instance, perhaps only specific traits are subject to the trade-off, as has been the common way to address the problem (Endler, 1995; Jennions *et al.*, 2001). Indeed, some studies on guppies have suggested trade-offs between mating success and viability for colour – commonly inferred as conspicuousness. That is, while some studies demonstrate that colour patterns are sexually selected (Endler and Houde, 1995; Houde, 1997; Hughes *et al.*, 1999, 2013; Graber *et al.*, 2015), others show that colour patterns are also naturally selected (Godin and McDonough, 2003; Olendorf *et al.*, 2006; Weese *et al.*, 2010; Gordon *et al.*, 2015) – although few authors have looked at both aspects of selection within the same study.

At the same time, other studies have shown the promise of the performance-based approach for studying selection in guppies. In particular, it has been shown that populations differ in the overall ability of males to obtain mates (Endler and Houde, 1995; Schwartz *et al.*, 2010) and avoid predation (Magurran and Seghers, 1974, 1990; Dugatkin and Alfieri, 1992; O’Steen *et al.*, 2002; Templeton and



Shriner, 2004; Magurran, 2005). Moreover, in the many-to-one mapping aspect of traits to performance (Arnold, 1983; Lailvaux and Irschick, 2006; Irschick *et al.*, 2008), the compromise between natural and sexual selection can be – for the traits – avoided through ‘private signals’ visible to mates but not to predators (Zuk and Kolluru, 1998; Stoddard, 1999; Cummings *et al.*, 2003), as has been inferred for guppies (Millar *et al.*, 2006; Millar and Hendry, 2012). Thus, we still favour the expectation that trade-offs are more likely at the level of whole-organism (performance) than at the level of the simple traits underlying that performance.

Fifth, although trade-offs are a common expectation in evolutionary ecology, their occurrence, at any level, might not be as straightforward as expected or, alternatively, they might be very weak and therefore hard to detect – or require a very large sample size to be detected, as in the present study. More generally, searching for even the broadest trade-offs has been surprisingly ineffective – or at least highly variable in outcome. As an example, whole-organism performance often does not strongly trade-off between environments (Hereford, 2009), seemingly in contradiction to the typical expectation of local adaptation. Moreover, a trade-off between reproductive effort in a breeding season and post-breeding survival was not readily detected in a meta-analysis (Santos and Nakagawa, 2012). One likely reason for these failures to detect trade-offs is that individual ‘quality’ (e.g. condition, energy, or size) covaries positively with performance across multiple environments or contexts, even if those performances would trade-off with each other should that ‘quality’ somehow be standardized (de Jong and Noordwijk, 1992). In our case, for example, perhaps some males simply had more energy, and so were more successful in both attracting females and in avoiding predators. Finally, compensatory traits – that is, traits that compensate for the negative effects of sexually selected traits on performance abilities (Oufiero and Garland, 2007; Husak and Swallow, 2011) – might hide a trade-off between natural and sexual selection.

Sixth, as with any experiment, the specific methodologies and designs in our study, such as the size of tanks or selection of experimental males, might have been suboptimal for the hypothesis being tested. Furthermore, conditions in nature – the context in which we actually care about trade-offs – are clearly very different from those in the laboratory. In the wild, for instance, many more males and females are present at any given time, other predators are present, more opportunities are present for guppies to hide from predators, lighting conditions are different, and so on. Overall, however, we take some solace in the fact that previous studies have considered female choice and predator susceptibility in similarly unrealistic laboratory conditions – and so the above concerns do not apply specifically to our study. Nevertheless, it is clear that, at least under some conditions, the whole-organism performance trade-off between natural and sexual selection is either weak or absent.

Like many other investigators (Bell, 1980; Reznick, 1985; Stearns, 1989; Jennions *et al.*, 2001; Hereford, 2009; Kingsolver and Diamond, 2011), we expect fundamental trade-offs must exist, including between natural and sexual selection – and so we are puzzled by the above-noted frequent lack of support for trade-offs in the literature. This conjunction of strong expectation and yet frequent failure of empirical support was precisely why we hoped to solve the conundrum with our ‘whole-organism’ approach. Thus, we too are now forced to concede an at least temporary inability to clearly demonstrate what should be a fundamental trade-off that underlies the modern conceptions of the way evolution works. By presenting these (mostly) negative results from our whole-organism performance trade-off study, we hope to inspire other investigators in their approach to detecting trade-offs, yet are cautious as to its panacean potential.

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