

## Shoaling behaviour in the pygmy halfbeak *Dermogenys collettei* (Belontiiformes: Zenarchopteridae): comparing populations from contrasting predation regimes

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**Abstract.** Exotic species—especially predators—are a potential threat to native species communities and ecosystems worldwide. Introduced exotic species may cause changes in anti-predator behaviour of prey species, thus affecting prey individuals' time allocations for other crucial behaviours such as feeding and locating mates. To test this hypothesis, we investigated shoaling behaviour of the pygmy halfbeak, *Dermogenys collettei*, comparing populations with different degrees of exposure to an exotic predator (*Cichla orinocensis*). Contrary to predictions, halfbeaks exhibited shoaling behaviour in a low predation, forest stream habitat but not in a high predation, more open stream habitat. We argue that behavioural differences are likely driven by competition for resources leading to reduced shoaling, highlighting how costs and benefits of group-living affect population-level shoaling tendencies. *Dermogenys collettei* also did not increase shoaling behaviour when exposed to *C. orinocensis*, suggesting that adaptive behavioural responses to immediate predation risk are absent. We discuss the implications of our results for the conservation of small native freshwater fishes in Singapore and Malaysia and identify further areas of research on predator-prey interactions between exotic predators and indigenous aquatic fauna.

**Keywords.** Singapore, Malaysia, exotic predator, invasion biology, alien species

### INTRODUCTION

The number of exotic species introductions worldwide is rapidly increasing, mostly as a result of anthropogenic activities (Copp et al., 2005; Chiron et al., 2009). Once successfully established in an area outside their original distribution range, exotic taxa have the potential to cause adverse effects in native ecosystems, which include the extirpation of populations of native species or even driving those species to extinction altogether by various mechanisms (Mooney & Cleland, 2001; Clavero & García-Berthou, 2005). Native prey species tend to suffer disproportionately from predation by exotic predators, possibly due to what has been termed 'prey naïveté' (Salo et al., 2007; Sih et al., 2010), and

this problem is likely exacerbated in freshwater ecosystems, which are usually more isolated compared to terrestrial or marine ecosystems (Cox & Lima, 2006). Exotic predators may also induce changes in the behaviour of their (native) prey species, including increased predator avoidance (Mooney & Cleland, 2001) and altered mating behaviour (Bierbach et al., 2011). Taken together, predation can thus affect not only the strength and direction of natural selection but also sexual selection, with far-reaching consequences for the maintenance of genetic variability and population survival (Stenseth & Dunlop, 2009). Therefore, it is imperative to investigate behavioural changes of native prey species in response to exotic predators, especially in terms of defensive behaviours that could directly influence their survival and fitness.

One such behaviour is shoaling (sensu Pitcher, 1983), a common behaviour in teleost fishes, with up to 25% of species forming shoals throughout their adult life (Shaw, 1978), and many more species forming shoals at least as juveniles. Shoaling provides several benefits, including protection from predators (Krause & Ruxton, 2002; Grobis et al., 2013) and increased foraging success (Pitcher et al., 1982), but also conveys costs such as increased competition for food between shoal mates (Plath & Schlupp, 2008), and so teleost fishes form shoals only if the benefits of shoal formation outweigh the costs (Godin, 1986; Pitcher & Parrish, 1993). This appears to be the case in multiple families, including species of the Neotropical Poeciliidae, which are known to form shoals for predator defence (Seghers, 1974). An interesting aspect of shoaling in poeciliids is that they display

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different levels of shoaling depending on their familiarity with different predator types and the level of predation risk they experience in the wild (Botham et al., 2006; Huizinga et al., 2009). In Palaeotropical Southeast Asia, the members of the widespread family Zenarchopteridae (Lovejoy et al., 2004) share multiple similarities with the Poeciliidae, including ecological and life-history traits (Reznick et al., 2007), though little is known about their behaviour. What few behavioural studies exist focus mainly on courtship and reproductive behaviour, and are observational in nature (Kottelat & Lim, 1999; Magyar & Greven, 2007; Greven, 2010). Experimentally examining shoaling behaviour in the zenarchopterid *Dermogenys collettei* in the present study permits investigation of whether zenarchopterids also use shoaling as a defensive behaviour, and if their tendency to shoal is influenced by familiarity with (exotic) predators.

The Malayan pygmy halfbeak (*Dermogenys collettei*) is a relatively widespread zenarchopterid that occurs from Sumatra to the north-western portion of Borneo (Sarawak, Brunei and north-western Kalimantan), as well as southern Peninsular Malaysia (Johor, Pahang) and Singapore (Meisner, 2001). *Dermogenys collettei* can be found in a wide range of habitat types, from pristine forest streams and estuarine habitats as found on Pulau [= island] Tioman (Ng et al., 1999; referred to as *D. pusilla*) to heavily disturbed environments dominated by exotic predatory species, as encountered in the city-state of Singapore (Ng et al., 1993; Tan et al., 2010; Baker & Lim, 2012), rendering it a prime candidate for investigating the influence of exotic predators on shoaling behaviour. Our present study asked (1) whether *D. collettei* displays intrinsic shoaling behaviour, (2) whether this behaviour varies with predation regime, and (3) whether the presence of an exotic predator (the peacock bass, *Cichla orinocensis*) leads to increased shoaling in populations that are familiar with this predator type.

To investigate intrinsic shoaling behaviour, shoal choice experiments were conducted to quantify the tendency to associate with conspecifics. We contrasted the behaviour of fish from habitats in which exotic predators have been introduced against fish from habitats where such predators are (as yet) absent. Shoal choice experiments were then repeated while a video stimulus of an exotic predator was presented, allowing us to determine potential predator-induced changes in shoaling behaviour. We hypothesized that halfbeaks from habitats with intense predation by peacock bass would exhibit stronger shoaling behaviour. Moreover, they should exhibit a marked increase in shoaling tendency when presented with a predator stimulus, owing to the recognition of a familiar predator type.

## MATERIAL AND METHODS

### Study sites and maintenance of study organisms.

*Dermogenys collettei* were collected from two locations on the island of Singapore (Lorong Banir and Jurong River), and from two locations on Pulau Tioman, located off the east coast of Peninsular Malaysia (Sungai [= river] Paya and Sungai Paya Kecil). The Singaporean locations (Lorong

Banir and Jurong River) are presently strongly affected by anthropogenic disturbances and are connected to artificial reservoirs that harbour feral populations of piscivorous South American peacock bass (*C. orinocensis*; Ng & Tan, 2010). This exotic predator can cause a massive alteration in ecosystem function once successfully established (Zaret & Paine, 1973; Pelicice & Agostinho, 2009). Conversely, the streams on Pulau Tioman (Sungai Paya and Sungai Paya Kecil) are largely unaffected by human activities (Jasmi, 1999), and are not known to contain any exotic predators (Ng et al., 1999). In addition, the native predators such as the Tioman walking catfish (*Clarias batu*) are benthic, euryphagous predators which feed on a wide range of prey, including insects and crustaceans (Lim & Ng, 1999), unlike more specialised piscivores like the peacock bass. This suggests that overall predation pressure on pelagic *D. collettei* on Pulau Tioman would be lower than in Singapore.

Shoaling experiments were carried out between July 2012 and January 2013. Halfbeaks were captured using  $0.6 \times 0.4$  m push nets (mesh size  $2 \times 2$  mm) and afterwards kept in well-aerated 70 litre tanks under a 12h:12h light:dark cycle and fed daily with live brine shrimp nauplii. Fish from Pulau Tioman remained on the island throughout the experiments involving them, with no living material being transferred to Singapore. In Singapore, the tanks were located in the Freshwater Aquarium holding facilities of the National University of Singapore, with fewer than 40 fish held in a single tank ( $90 \times 40 \times 30$  cm). All fish were acclimated to laboratory conditions for at least one day before they were tested. Upon completion of the experiment, all fish were released at their site of origin. Collection and maintenance procedures were in accordance with National University of Singapore Institutional Animal Care and Use Committee guidelines (IACUC protocol #B05/12).

**Shoaling experiment.** The experimental setup to quantify shoaling tendencies was modified from Bierbach et al. (2011). The experimental tank ( $90 \times 40 \times 30$  cm), made from UV-transparent Plexiglas, was divided length-wise into three equal zones, with the central zone designated as the neutral zone and two preference zones on either side. It was filled with treated tap water up to a depth of 15 cm. Two smaller auxiliary Plexiglas tanks ( $20 \times 20 \times 30$  cm) were placed at both ends, adjacent to the preference zones, one of which would later contain the stimulus shoal (Fig. 1A). The setup was observed at a distance of two metres so as to minimise the observer's influence on the behaviour of the test fish. The outer sides of the tank (except the front) were covered with opaque black plastic film to further minimise disturbance. A small section at the back of the tank was left uncovered for a video monitor displaying a video of a predator during the predation treatment (see below).

During the tests, one auxiliary tank contained a shoal of four individuals while the other was left empty; we alternated the side at which the shoal was situated at the beginning of a trial. Stimulus fish were obtained from the same holding tank as the focal fish whenever possible. To initiate a trial, a focal individual was introduced into the neutral zone of

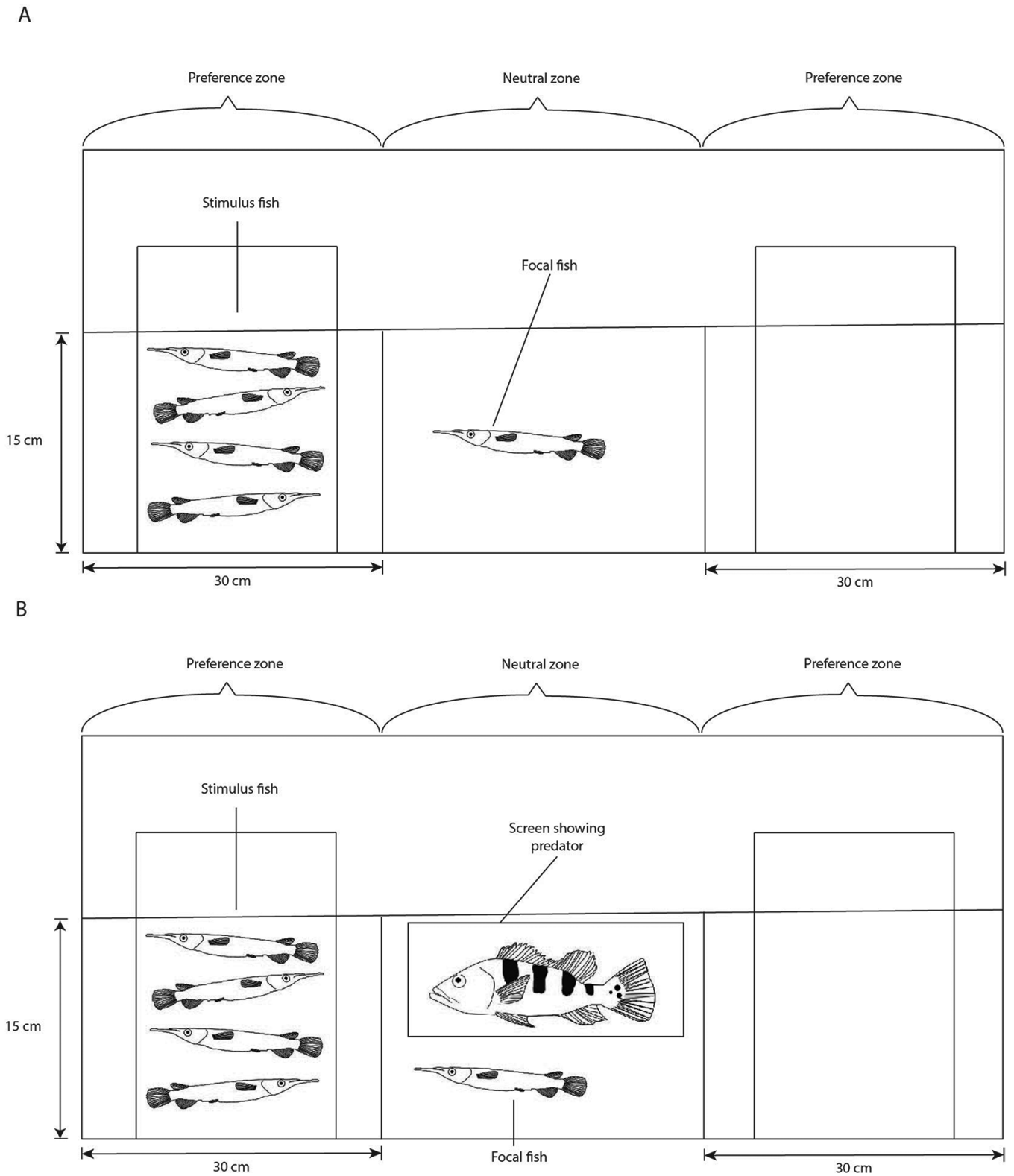


Fig. 1. A, Experimental set-up to determine shoaling tendencies. During the first part of the experiment, no digital screen was present; B, during the second part, a predator was displayed on the screen.

the tank (Fig. 1A). Each trial began after an acclimatisation period of five minutes, or when the focal individual started to swim freely. We recorded the time the focal individual spent in each preference zone during a five-minute period. Subsequently, the two auxiliary tanks were exchanged and testing was repeated to control for side biases. These two five-minute periods constitute the first part of the shoaling experiment.

In the second part of the experiment, the testing procedure was repeated while the video of a slowly moving predator (*C. orinocensis*) was displayed on a screen (Sony Digital Photo Frame D1020, 10", 800 × 480 pixels) placed against the posterior wall of the test tank, centrally in the neutral zone (Fig. 1B). We did not use live specimens due to logistical and ethical issues associated with transporting an exotic predator to Pulau Tioman (where it may be inadvertently introduced). Other studies, however, have successfully used models or videos to simulate predators in similar experiments (Magurran & Girling, 1986; Johnson & Basolo, 2003), and multiple studies confirm that fish display similar responses to both videos and living individuals (Balshine-Earn & Lotem, 1998; D'earth, 1998; Clark & Stephenson, 1999). We also conducted negative controls, so half of the tests were run without presentation of the predator in the second part of the experiment. The videos were modified from a source on the internet (Liu, 2010), with a sequence of 5 seconds (1.01–1.06 in the video) being cut and looped to represent the predator calmly swimming from one side of the tank to the other.

Each 20-minute trial only involved individuals of the same sex and from the same sampling site. Throughout the study, each focal individual was only tested once. However, owing to the limited number of fish available, some focal individuals were used as stimulus individuals at least a week after they were first tested. At the end of each trial, the total length of the focal and the stimulus individuals were recorded to the nearest millimetre using a pair of dial callipers. In total, 24 trials were carried out for each combination of sex and location for the predator treatment, while 15 trials were carried out for each of the corresponding control runs, amounting to a total of  $N = 312$  trials.

**Data analysis.** All statistical analyses were carried out with R version 3.0.2 (R Development Core Team, 2013). Our data violated both the assumptions of normal distribution (tested using Shapiro-Wilks' tests) and homoscedascity (tested using Levene's tests), even after applying different transformation methods. Therefore, we used a generalised linear model to determine if shoaling tendencies differ between sites and sexes (fixed factors), and if focal body size (FBS) and mean stimulus body size (MSBS) had an effect (covariates). A shoaling score (the difference between time spent in the compartment with the shoal and time spent in the empty compartment) was used as the dependent variable. The output from a Wilcoxon rank-sum test suggests that there were no significant differences in shoaling tendencies between the two Malaysian sites ( $W = 3400.5$ ,  $p = 0.204$ ), as well as between Singaporean mainland populations ( $W = 2744$ ,  $p = 0.343$ ), so all data from the same country were

pooled. The interaction terms that were considered in the model were site\*sex, FBS\*MSBS, site\*FBS\*MSBS, and sex\*FBS\*MSBS, where asterisks (\*) indicate interactions. The full model used was Shoaling Score~Sex + Site + Setup + Sex\*Location + FBS + MSBS + FBS\*MSBS + Sex\*FBS\*MSBS + Location\*FBS\*MSBS. Step-wise model elimination was then carried out to remove any insignificant interaction terms and variables.

Likewise, in order to determine the change in shoaling tendencies in the presence of a predator, the shoaling score for the first half of the experiment was subtracted from the shoaling score of the second half, and the resulting score was analysed utilising a general linear model considering predator treatment as a fixed factor, while including all fixed factors, covariates and interaction terms (including interactions with 'treatment') used in the first model.

## RESULTS

**Population differences in shoaling tendencies.** The model indicated a significant difference in shoaling behaviour between fish originating from Malaysia and Singapore ( $t = -2.28$ ,  $\text{Pr}(>|t|) = 0.023$ ), and halfbeaks from Malaysia spent more time shoaling (Fig. 2). Halfbeaks from Singapore, by contrast, spent similar amounts of time close to the stimulus shoal and in the empty compartment (Fig. 2). Focal individuals' body size, average size of the shoal, and sex did not have a significant effect on the time spent by focal individuals in each compartment (Table 1A). Therefore, halfbeaks in Malaysia appear to display shoaling behaviour, but halfbeaks in Singapore do not.

**Predator-induced changes in shoaling tendencies.** The model indicated no significant change in preference scores between halfbeaks in Singapore and Malaysia ( $t = -0.52$ ,  $\text{Pr}(>|t|) = 0.61$ ). Additionally, no other factors or interactions were statistically significant (Table 1B). This demonstrates that halfbeaks from both Singapore and Malaysia did not display any significant change in shoaling behaviour between the first and second halves of the experiment upon exposure to an alien predatory fish stimulus.

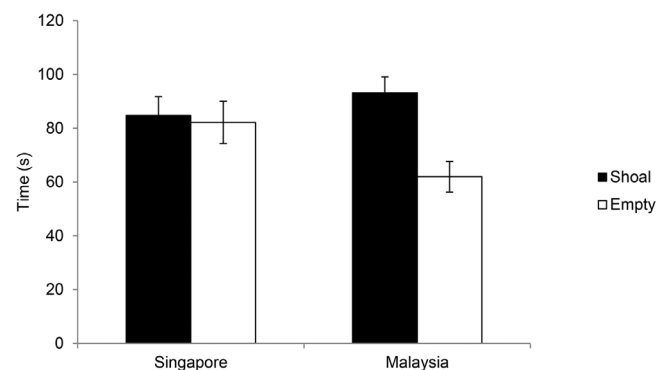


Fig. 2. Mean time individual *D. collettei* from Singapore and Pulau Tioman (Malaysia) spent in the shoaling and empty compartments;  $N=156$  trials for each location (Total  $N=312$  trials). Error bars show standard errors.

Table 1. Results of general linear models using: A, a shoaling score; B, the change in shoaling tendencies over the course of the experiment as the dependent variable. The models were simplified by removing insignificant variables and interaction terms. Focal Body Size refers to the length of the focal individual while Mean Stimulus Body Size refers to the average length of all individuals in the stimulus shoal.

**A**

Coefficients	Estimate	Std. Error	t-value	$Pr(> t )$
(Intercept)	31.144	8.847	3.520	0.000496
Singapore	-28.513	12.512	-2.279	0.023352

**B**

Coefficients	Estimate	Std. Error	t-value	$Pr(> t )$
(Intercept)	41.892	72.343	0.579	0.563
Singapore	15.336	22.109	0.694	0.488
Focal Body Size	8.135	8.527	0.954	0.341
Mean Stimulus Body Size	-18.877	18.375	-1.027	0.305



Fig. 3. Sampling sites in Singapore and on Pulau Tioman, Malaysia. A, Lorong Banir, Singapore; B, Jurong River, Singapore; C, Sungai Paya, Pulau Tioman, Malaysia; D, Sungai Paya Kecil, Pulau Tioman, Malaysia.

## DISCUSSION

**Population differences in shoaling tendencies.** Predation has been acknowledged as a prime mechanism by which natural selection affects the evolution of populations (Endler, 1986; Abrams, 2000), and reduced predation risk is the primary benefit arising from shoaling behaviour (Pitcher & Parrish, 1993; Magnhagen & Magurran, 2008). However, contrary to our prediction, *D. collettei* from Pulau Tioman (Malaysia), which we classified as a low predation environment, displayed shoaling behaviour, while those found in the high predation environment of Singapore did not. This result was unexpected as most other fish populations exposed to high predation risk show stronger anti-predator responses, especially shoaling (Botham et al., 2008; Kozak & Boughman, 2012). While studies on Trinidadian guppies (*Poecilia reticulata*) also found different levels of shoaling among geographically separated populations that face similar predation risk (Magurran et al., 1993), such populations often also displayed significant amounts of genetic divergence. Preliminary genetic analyses, however, indicate that the halfbeak populations in Pulau Tioman and Singapore do not exhibit pronounced genetic divergence (0.03–0.05% uncorrected pairwise distance for a 605 basepair COX1 fragment; Y. Yi & S. Klaus, unpublished data).

A possible explanation for different shoaling behaviour between *D. collettei* populations would be that it is caused by trade-offs between the costs and benefits of shoaling. In other words, not only differences in potential benefits between populations affect the evolution of shoaling behaviour (Pitcher et al., 1982; Morgan & Godin, 1985), but also differences in the cost of shoaling (Plath & Schlupp, 2008; Herczeg et al., 2009). If the benefits do not outweigh the costs of shoaling in a given population, shoaling is likely to be lost (e.g., Plath & Schlupp, 2008). Indeed, hungry fish have been shown to reduce their shoaling tendencies, probably to minimise intraspecific competition (Krause, 1993; Reeb & Saulnier, 1997).

While shoaling can increase the rate at which fish locate food (Pitcher et al., 1982), this may not be applicable to all species. Previous studies have examined species that forage in the entire water column including the bottom; for such species, food resources tend to be scattered but food patches satisfy multiple individuals (Pitcher & Parrish, 1993; Krause & Ruxton, 2002). However, when discrete, singular food items are more evenly dispersed, most fish tend to reduce shoaling (Morgan, 1988; Miller & Gerlai, 2007). Species in the genus *Dermogenys* mainly feed on terrestrial insects falling onto the water surface (Ward-Campbell et al., 2005). Therefore, it is conceivable that shoaling does not confer substantial foraging benefits on *D. collettei*, and instead might increase competition for food in Singapore's streams, which possess degraded riparian vegetation (Fig. 3A, B; Corlett, 1992; Tan et al., 2010). Pulau Tioman, in contrast, has been gazetted as a wildlife reserve area, and natural canopy cover around its streams is intact (Fig. 3C, D; Jasmi, 1999). Allochthonous nutrient input (especially in terms of insects) into such forest stream systems was found to be significantly higher than in

more open stream systems that lack overhanging or riparian vegetation (Edwards & Huryn, 1996; Kawaguchi & Nakano, 2001; Baxter et al., 2005).

A word of caution is required, as the main predators of halfbeaks may not be aquatic but avian predators instead. As halfbeaks spend most of their time just below the surface, they are likely to be easily spotted by piscivorous birds like the collared kingfisher (*Todiramphus chloris*) or the little heron (*Butorides striatus*), which are found in both Singapore (Davison & Yeap, 2010) and Pulau Tioman (Sodhi et al., 1999). Fish shoals are easily spotted from the air (Pitcher & Parrish, 1993), and shoals of surface-dwelling fish should be even easier for avian predators to locate and consume. However, fish also increase shoaling behaviour when encountering avian predators (Pitcher et al., 1988; Litvak, 1993), and so it is possible that increased shoaling on Pulau Tioman is a response to avian predation. Future studies will have to elaborate on this idea and provide quantitative data on bird predation risk and avian capture rates (e.g., Allouche & Gaudin, 2001; Riesch et al., 2010).

In other species such as zebrafish (*Danio rerio*) and guppies (*Poecilia reticulata*), shoaling behaviour differs between sexes, and males tend to shoal less (Griffiths & Magurran, 1998; Ruhl & McRobert, 2005). In the current study, there appeared to be no significant differences in shoaling tendencies between male and female halfbeaks, which is consistent with field observations of mixed-sex groups in the wild (Greven, 2010). While male *D. collettei* are reported to be aggressive towards other males (Baker & Lim, 2012), no incidents of male–male aggression were observed throughout the course of our study, and so aggression might play a role only when males attempt to form dominance hierarchies, which was unlikely to occur under the experimental conditions used in our present study.

Body size also plays a vital role in shoaling decisions in other fish species, with fish generally preferring to shoal with similar-sized individuals (Hoare et al., 2000). This is thought to be driven by the 'oddy effect', where individuals that are dissimilar from other shoal mates are more easily targeted by predators (Landeau & Terborgh, 1986). However, in our study, body size had no significant effect on shoaling behaviour in *D. collettei*. This is consistent with the suggestion that shoaling behaviour in *D. collettei* is not only a predator defence mechanism but also assists in mate finding (Ruhl & McRobert, 2005), as smaller individuals can have directional mating preferences for larger mates (Dosen & Montgomerie, 2004; Godin & Auld, 2013).

**Exotic predator recognition.** The results of our study also indicate that halfbeaks from both Malaysia and Singapore did not display any significant change in shoaling preference when exposed to *C. orinocensis*. This likely indicates that *C. orinocensis* is not recognised as a predator by *D. collettei*, a not unexpected result for the Pulau Tioman population, since *C. orinocensis* is not present there (Ng et al., 1999). However, *C. orinocensis* is present at Lorong Banir (unpublished data) and is likely present in the Jurong River (Ng & Tan, 2010).

Therefore, it appears that halfbeaks in Singapore are still predator-naïve with regards to *C. orinocensis*.

A possible reason for this apparent naïveté is that the peacock bass is simply not recognised as a threat by *D. collettei*. While other shoaling fish display anti-predator behaviour even when exposed to novel predators (Hawkins et al., 2004; Botham et al., 2006), *D. collettei* appears to be an exception. This suggests that the pygmy halfbeak does not possess a general anti-predator response, unlike other shoaling fish occupying similar ecological niches like the poeciliids (Botham et al., 2006). However, it should be noted that studies conducted in other locations where *Cichla* were introduced indicate that native fish there do recognise *Cichla* as a novel threat and display anti-predator responses, but are still vulnerable to predation by it (Kovalenko et al., 2010). However, native species of cichlids were present in those sites studied, and it is possible that *Cichla* were similar enough to native predators to trigger anti-predator responses in native prey species. In contrast, there are no close relatives of *Cichla* occurring naturally in Southeast Asia (Kottelat, 2013). Several studies (Brown & Warburton, 1999; Bass & Gerlai, 2008) have also shown that fish tend to ignore or inspect novel allopatric predators when initially exposed to them. Additionally, *C. orinocensis* is a fast-swimming predator which actively hunts throughout the water column (Winemiller et al., 1997), unlike most native predatory freshwater fishes in Singapore and Pulau Tioman (Ng et al., 1999; Baker & Lim, 2012). Thus, it is likely that *D. collettei* did not recognise *C. orinocensis* as a threat, and therefore did not display any change in behaviour. Alternatively, *C. orinocensis* may so far be relatively uncommon in Singapore streams, making it possible that the halfbeaks in Singapore simply have not been exposed (or exposed frequently enough) to predation from them, and therefore did not change their behaviour in an adaptive way. Thus, a fruitful area of research in the future would be to examine the capability of *D. collettei* to learn to recognise an unfamiliar predator, since research suggests that several other fishes develop anti-predator responses via experience and learning (Kelley & Magurran, 2003; Ferrari & Chivers, 2006).

In addition, this study focused solely on the response to visual cues from a piscine predator. It is possible though, that *D. collettei* responds to other cues instead to determine whether or not a predator poses a threat, such as olfactory (Brown et al., 2000; Kelley & Magurran, 2003) or mechanical cues (Engelmann et al., 2000).

**Conservation aspects.** The results of this study carry implications for the conservation of *D. collettei*, especially in Singapore. The lack of response towards an exotic predator by *D. collettei* suggests that the species is currently vulnerable to exotic predators. This could affect Singaporean populations dramatically in the short term. The situation may change if the population of *D. collettei* learns to recognise new predators, but damage may have already been done by then. It has been shown that the introduction of exotic species into aquatic ecosystems can dramatically alter existing food webs (Vander Zanden et al., 1999), which

can lead to a cascade effect in the ecosystem. If allowed to continue, the composition of the community may change so drastically that in the worst case scenario, the ecosystem may completely collapse as species become extirpated or go extinct (Goldschmidt et al., 1993; O'Dowd et al., 2003). Thus, it is imperative that any existing population of exotic species be monitored carefully, especially in locations like Singapore, where the freshwater ecosystems are already stressed from the effects of development and urbanisation. Limiting the spread and impacts of exotic species is an extremely important part of managing such environments, and if neglected, could have severe effects. However, if sufficient care is taken, any negative impact from such species can be minimised or even avoided altogether, and the native ecosystems maintained in as good a condition as possible (Mack et al., 2000).

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