

## Exploratory behaviour and transmission of information between the invasive guppy and native Mexican topminnows

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Sociability in animals provides benefits such as reduced predation risk and increased foraging efficiency. During the early stages of invasion, individuals are often vulnerable as part of a small population (Allee effects); associations with native heterospecifics could mitigate some of the disadvantages of small population size and thereby increase the chances of establishment success. Here we explored two potential benefits of heterospecific association to guppies, *Poecilia reticulata*, a very successful invasive species. We first investigated whether guppies can exploit visual cues from morphologically similar heterospecific individuals as effectively as those from conspecifics. We next tested whether willingness to explore an unfamiliar environment depends on whether guppies are accompanied by conspecifics or heterospecifics. Our results show that guppies can acquire information on food availability from another species, as well as from conspecifics. We also found that guppies engaged in exploratory behaviour more quickly if the habitat had plants in it, and were more likely to associate if it was unstructured; there was, however, no difference in the frequency with which the focal fish was accompanied by a conspecific or a heterospecific individual. These results show that guppies respond to these heterospecifics as they do with conspecifics. Our study reveals some of the traits that could make an invader successful and potentially help to identify species with a higher potential to become established outside their native range.

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Allee effects manifest as a reduction in viability at low population densities, i.e. an individual's fitness will be lower when there are fewer conspecifics around (Stephens, Sutherland, & Freckleton, 1999). They can be caused by a variety of mechanisms, including less efficient predator avoidance, difficulties in finding mates or limited reproductive facilitation in colonial breeders (Couchamp, Berec, & Gascoigne, 2008). Allee effects may play a role in the extinction of already endangered species; moreover, by the same token, they affect the dynamics of invasive species (Taylor & Hastings, 2005; Tobin, Berec, & Liebhold, 2011).

Invasive species are recognized as one of the greatest threats to biodiversity (Garcia-Berthou, 2007; Simberloff et al., 2013) and may change the environment in multiple ways (Simon & Townsend, 2003) leading to loss of native species and wildlife homogenization (Moyle, 1996; Simberloff et al., 2013; Strayer, 2012; Vitousek, Dantonio, Loope, Rejmanek, & Westbrooks, 1997). Biological invasion tends to begin with a few individuals arriving in an unknown

environment (Mack et al., 2000); founding individuals thus often have to face Allee effects (Tobin et al., 2011). Behaviour may play a crucial role in enabling such individuals to compensate for Allee effects when invading and to survive until they can reproduce (Holway & Suarez, 1999; Stephens & Sutherland, 1999). Behaviour is more plastic than life history or morphological traits, and therefore it is more likely to provide solutions to increasing survival in a novel situation (Magurran, 1999).

The most common associations are between individuals of the same species (Krause & Ruxton, 2002). Associations between different species, however, occur in many taxa, and have been reported in primates (Stensland, Angerbjorn, & Berggren, 2003), birds (Powell, 1989) and fish (Camacho-Cervantes, Ojanguren, Deacon, Ramnarine, & Magurran, 2014; Ward, 2012). The benefits of grouping extend to heterospecific associations as well as conspecific ones (Barakat et al., 2009; Frank, 1994). For example, it has been demonstrated that Carib grackles, *Quiscalus lugubris*, learn as readily from a Zenaida dove, *Zenaida aurita*, as they do from a conspecific (Lefebvre, Templeton, Brown, & Koelle, 1997). In fish, behavioural responses to heterospecific chemical alarm cues promote predator avoidance (Chivers, Mirza, & Johnston, 2002).

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Associating with heterospecifics could be particularly beneficial in situations in which there are not many conspecifics present, in which case a heterospecific partner might be the second best option. For example, efficient foraging requires information on where to forage and how long to spend at each patch. This information can be obtained directly, by sampling, or indirectly by attending to social cues produced intentionally or inadvertently by other individuals (Kendal, Coolen, van Bergen, & Laland, 2005), which in the invasion scenario could potentially be native species.

The Trinidadian guppy, *Poecilia reticulata*, has managed to invade more than 70 countries (Deacon, Ramnarine, & Magurran, 2011), including the Mexican Central Plateau. In this area of Mexico, freshwater bodies are inhabited by species that have a strong endemic component; among these taxa the Goodeidae family is one of the most threatened (De La Vega-Salazar, Avila-Luna, & Macías García, 2003; Domínguez-Domínguez, Martínez-Meyer, Zambrano, & De Leon, 2006; Magurran, 2009). Goodeids are freshwater topminnows, which inhabit mostly shallow lakes and rivers, are largely omnivorous and are viviparous. They are morphologically similar to guppies and share ecological niches (Valero, Macías García, & Magurran, 2008). Moreover, some population declines have been directly attributed to guppy invasion (De La Vega-Salazar et al., 2003; Valero et al., 2008; Valero, Magurran, & Macías García, 2009).

In previous experiments, we found that guppies associate with heterospecific individuals (Camacho-Cervantes, Ojanguren, et al., 2014) and by doing so they are able to increase their shoal size, locate food faster and spend more time foraging (Camacho-Cervantes, Macías García, Ojanguren, & Magurran, 2014). To identify the mechanisms by which invasive guppies gain benefits from heterospecific associations, we assessed their ability to acquire information on food availability by observing the behaviour of heterospecifics and to explore an unknown habitat with an individual of a different species. In the first experiment (transmission of information) we investigated whether individual guppies changed their behaviour when watching groups of fish that had chemical information on food availability. In the second experiment (exploratory behaviour) we tested the willingness of guppies to explore environments with and without plants when associating with either another guppy or a heterospecific individual. For both experiments, we used butterfly splitfins, *Ameca splendens*, a species of goodeid native to freshwater habitats of the Mexican Central Plateau where the guppies are invading. Moreover, both species share ecological requirements and have a similar phenotype. We predicted that being able to acquire information and explore unknown environments when accompanied by butterfly splitfins could provide guppies with more foraging opportunities and potentially increase their chances of becoming established.

## METHODS

Guppies used in these experiments were part of the University of St Andrews research aquarium and butterfly splitfins were part of the St Andrews Aquarium collection. Both were descendants from wild individuals collected in their native habitats (the lower Tacarigua river in Trinidad and the headwaters of the Teuchitlán river in Mexico, respectively) several years ago. Fish were kept in stock tanks (45 litres) that contained between 20 and 25 fish. Water in these tanks was continuously aerated and filtered and the tanks were furnished with gravel, rocks and plastic plants. Water temperature was kept at about 23 °C (ranging from 20 to 26 °C) and the photoperiod was 12:12 h light:dark from 0800 to 2000 hours. All observation trials were conducted from March to November 2013 at the University of St Andrews, U.K.

Experimental fish of each species were kept in separate stock tanks for at least 3 weeks prior to the start of the experiment to avoid familiarity effects (Griffiths & Magurran, 1997). Fish were fed once a day with Tetramin flakes a minimum of 12 h before the trials to ensure the fish showed food-searching behaviour. As butterfly splitfins are significantly bigger than guppies when they reach adulthood, we decided to use juveniles, which resemble guppies in size, colour and aggregation behaviour. Although we cannot exclude the possibility of age- or sex-specific effects, mixed-species shoals of guppies and other taxa are widespread in both Trinidad and Mexico (personal observation) and almost invariably include individuals at different developmental stages. In addition, the choice of female subjects reflects the fact that, in the case of guppies, females allocate more time to social behaviour than males (Sievers et al., 2012).

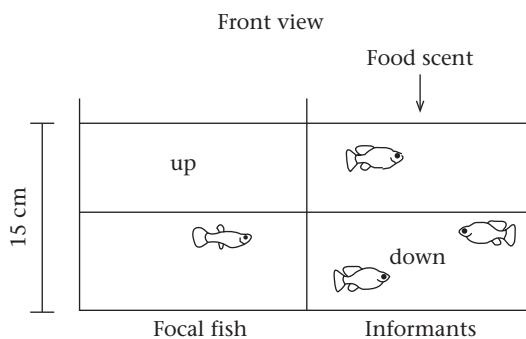
### Transmission of Information

We explored the ability of guppies to acquire information by observing the swimming pattern of butterfly splitfins that knew that food was available. The focal fish was always a female guppy and informants were either three female guppies or three juvenile butterfly splitfins in an adjacent tank that received a food cue. We tested the response of focal guppies to the change in swimming behaviour of an informant shoal after receiving a chemical food cue. For the purpose of this experiment we placed the focal guppy in a tank (20 × 30 cm and 15 cm high) and the informants in an identical adjacent tank, so both could see each other but with no exchange of chemical cues (Fig. 1). To make the informants aware of the presence of food, we prepared food-scented water by adding 5 g of Tetramin flakes to 100 ml of clear water and removing the flakes sediment after 5 min.

Trials took place between 1000 and 1500 hours and each trial lasted 16 min. The observation tank was filled with water to a depth of 15 cm. Pilot studies confirmed that 'snapshot' observations were an effective method of recording these behaviours. Accordingly, every 20 s we recorded the position of the focal and informant fish as up (closer to the water surface) or down (closer to the bottom). After the first 8 min we gently added a single dosage of 8 ml of scented water (food cue) with a syringe in the informants' tank and observed the change in the fish's vertical swimming pattern.

After every trial, water in both tanks was discarded and replaced with clean water. In between trials, focal fish were kept in a stand-by tank for 30–40 min. Fish for the shoals were haphazardly selected for each trial from a pool of 23 fish per species to avoid pseudoreplication (Hurlbert, 1984).

We used a repeated measures approach in which 21 focal fish performed two trials: one with three butterfly splitfins and the



**Figure 1.** Transmission of information experiment: diagram of the tank set-up. Fish were considered up when within 7.5 cm below the water surface or down when within 7.5 cm above the tank bottom.

other with three guppies as informants. The order in which trials were presented to each focal fish and the side of the tanks used for trials were randomized. To exclude the possibility of the focal fish obtaining information from the environment rather than from the other fish, we carried out a control in which there were no fish in the informants' tank; these observations were recorded in the same way as the experimental trials by injecting scented water into the empty informants' tank. Additionally, to control for social cues, we carried out a fourth treatment with conspecifics as informants and injecting only unscented water into the tank.

### Exploratory Behaviour

We set up an observation tank (40 × 30 cm and 30 cm high) that included gravel on the bottom and a transparent plastic container (bottle) with a window opening (5 × 6 cm) on the side at the bottom. Focal fish (always a guppy) and shoaling partner (either another guppy or a butterfly splitfin) were gently released inside the bottle and were given up to 15 min to exit the bottle through the window and explore the rest of the tank. We assumed behaviour was exploratory when the focal fish, and the shoaling partner, exited the bottle through the window, as the area outside the bottle was unknown to them. Once both fish had exited the bottle we observed them for 8 min, recording the distance between the two fish every 20 s. We carried out 38 observation trials in which the fish were presented with an environment with plants and 38 in an environment without them (Fig. 2). From the 38 observation trials for each treatment, 19 had a guppy as a shoaling partner and 19 had a butterfly splitfin. The tank with plants contained three green plastic aquarium plants 15 cm tall, with three branches, and about 29 cm diameter at the widest part when under the water. Each focal fish was used only once and therefore all observations were independent from each other.

### Ethical Note

The experiments were approved by the University of St Andrews Animal Welfare and Ethics Committee (2011). We used about 100 female guppies and about 50 juvenile butterfly splitfins. The experimental design involved observations of shoaling behaviour in glass aquarium tanks, and did not include any surgery, anaesthesia or other invasive procedure that could have caused distress or pain in the fish. Mortality was negligible (<10%) and once the experiments were completed, fish were returned to their original aquaria and kept for further experiments.

### Data Analysis

The focal individual's size relative to that of the informants in the transmission of information experiment was not significantly

different whether the shoal was composed of guppies or butterfly splitfins (ANOVA:  $F_{1,42} = 0.47$ ,  $P = 0.830$ ) and focal fish and shoaling partners of both species in the exploratory behaviour experiment were size matched (ANOVA:  $F_{1,72} = 2.39$ ,  $P = 0.12$ ) to avoid size-biased results. Moreover, preliminary analyses showed that size had no effect on the number of times the focal fish were found in the upper part of the tank (linear mixed-effect model (lme):  $F_{5,73} = 0.054$ ,  $P < 0.816$ ). Similarly, exploratory behaviour analyses included size as a variable: this had no effect on the focal fish behaviour (ANCOVA:  $F_{1,44} < 1.21$ ,  $P > 0.279$ ). Size was therefore not included in subsequent analyses.

In the transmission of information experiment, an lme model was used to test for the change in focal fish's behaviour when we injected scented water in the informants' tank and the informants were either three guppies or three butterfly splitfins. We next used an lme model to examine the change in informants' behaviour (Pinheiro, Bates, DebRoy, Sarkar, & R-Core-Team, 2013; Venables & Ripley, 2002); to confirm they were perceiving the chemical cue, we recorded every time at least two of the three fish were in the upper section of the tank. Finally, we carried out a Tukey post hoc (glht) analysis to find out whether control treatments were different from the experimental treatments and if there was a difference between guppies and splitfins as informants (Genz et al., 2013; Hothorn, Bretz, & Westfall, 2008).

In the exploratory behaviour experiment, to explore the willingness of heterospecific or conspecific pairs to explore the given environment (simple or complex), we performed binomial tests for the difference in the proportion of times a guppy or a butterfly splitfin exited the bottle first. Next, we examined differences in the species of the first fish to exit the bottle when there were and were not plants outside the bottle, also using binomial tests. We used ANOVA to test for the effect of habitat (with or without plants) and partner species on the time it took the focal fish to exit the bottle and the difference between the focal fish's and the partner's time. Finally, we used an ANOVA to test for differences in the times the two fish were found within one body length from each other when the partner was another guppy or a butterfly splitfin in an environment with or without plants. All analysis were performed using the R statistical software (R Core Team, 2013).

## RESULTS

### Transmission of Information

Test results showed that, as expected, informants were more often found in the upper part of the tank after the food scent was injected (lme:  $F_{5,79} = 150.06$ ,  $P < 0.001$ ). In addition, in the control trial with unscented water, the swimming pattern (up or down) did not change (glht:  $Z = 0.311$ ,  $P = 0.999$ ). After informants had received the food cue, focal fish had a higher tendency to swim in

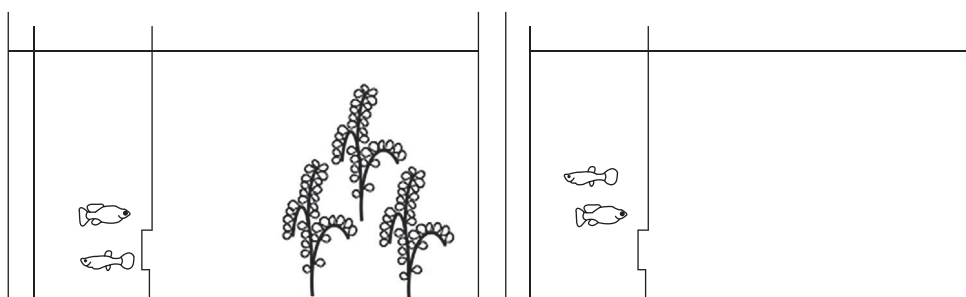


Figure 2. Exploratory behaviour experiment: diagram of the tank set-up. Tank with plants contained three plants with three branches each.

the upper part of the tank, and were found there more often than before the food scent was introduced (lme:  $F_{7,119} = 79.52$ ,  $P < 0.001$ ). Focal fish behaved in the same way irrespective of whether the informants were other guppies or butterfly splitfins (post hoc Tukey HSD analysis: glht:  $Z = 0.908$ ,  $P = 0.985$ ). In addition, post hoc analysis revealed a significant difference between experimental and control trials (glht:  $|Z| > 13.221$ ,  $P < 0.001$ ; Fig. 3).

Exploratory Behaviour

Fish were more likely to leave the refuge and explore the habitat when this was more complex regardless of the species of the partner and there was no difference in the species of the first fish to leave the refuge in either of the two habitats (Table 1). The time between the focal fish and the partner exiting the bottle was not affected by the species of the partner (ANOVA:  $F_{1,45} = 0.27$ ,  $P = 0.604$ ), nor by the complexity of the habitat (ANOVA:  $F_{1,45} = 0.73$ ,  $P = 0.397$ ). Habitat complexity had an effect on the time it took the focal fish to leave the refuge: in more complex habitat fish exited the bottle faster (ANOVA:  $F_{1,48} = 5.23$ ,  $P = 0.027$ ; Fig. 4) but there was no effect of the partner species (ANOVA:  $F_{1,48} = 0.65$ ,  $P = 0.422$ ; Fig. 4).

There was a significant effect of habitat complexity on how often fish were found within one body length from each other after both left the refuge: fish were more willing to associate in the simpler habitat (ANOVA:  $F_{1,45} = 50.43$ ,  $P < 0.001$ ; Fig. 5), but species of the partner did not have any effect (ANOVA:  $F_{1,45} = 0.63$ ,  $P = 0.431$ ; Fig. 5).

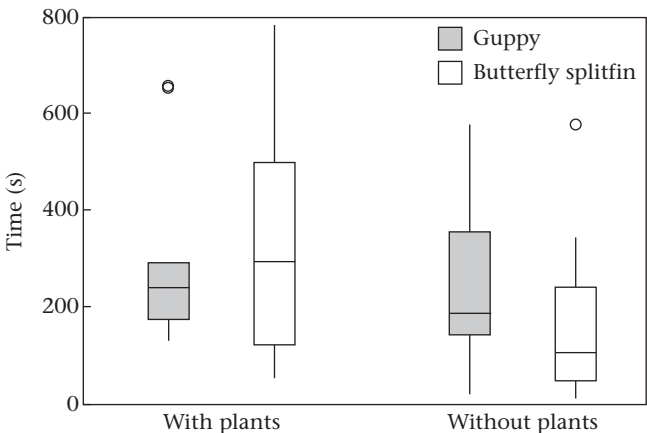
DISCUSSION

Invasion success depends on the ability of invaders to cope with the novel conditions they will encounter outside their native range; these include unknown food sources, predators and competitors (Sax et al., 2007). Guppies are able to derive foraging benefits from native Mexican topminnows (Camacho-Cervantes, Macias-Garcia, et al., 2014), although the mechanisms by which they are able to find food faster are unknown. In this study, we found for the first time that guppies are able to respond to heterospecific cues to the same extent as those from conspecifics. Moreover, guppies in our study were equally willing to explore an unknown environment whether their partner was another guppy or a butterfly splitfin.

**Table 1**  
The number of times both fish exited the bottle and the species of the fish that exited first

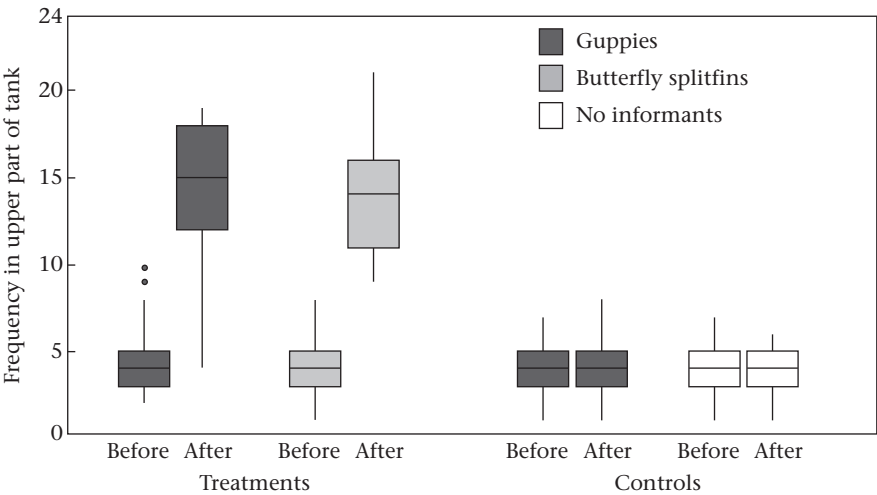
	Habitat		
	Simple	Complex	Z
No. of times both fish exited (maximum=19)			
<i>P. reticulata</i>	9	16	−2.39*
<i>P. reticulata</i> – <i>A. splendens</i>	8	16	−2.69**
Z	0.32	0	
Species of first fish to exit			
<i>P. reticulata</i>	5 (9)	8 (16)	0.27
<i>A. splendens</i>	6 (8)	9 (16)	0.89
Z	−0.83	0.35	

Differences were examined using binomial tests for difference in proportions. Numbers in parentheses are the maximum numbers of fish exiting the bottle. \* $P < 0.01$ ; \*\* $P < 0.001$ .



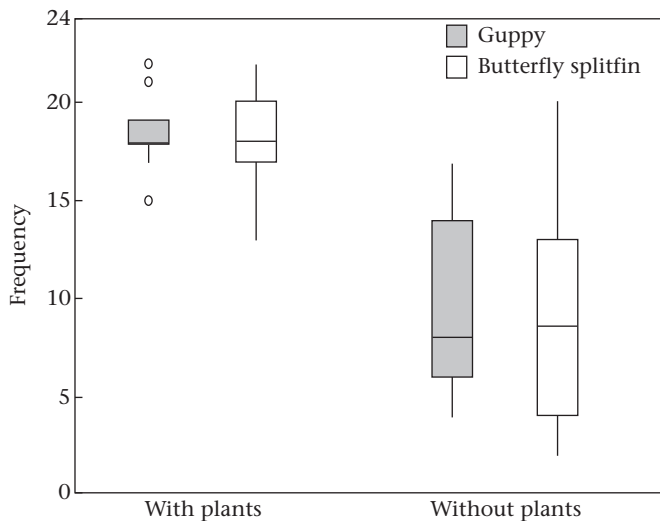
**Figure 4.** The time it took the focal individual to exit the bottle. Horizontal lines represent the median, boxes indicate interquartile ranges and vertical lines show the range excluding outliers (circles).

This could be particularly relevant for invasive species that are highly social, such as the guppy (Magurran, 2005), and typically occur in small numbers during the initial invasion stage (Mack et al., 2000).



**Figure 3.** The number of times the focal guppy was found in the upper part of the tank (maximum = 24) before and after the food scent was introduced into the informants' tank. In the guppy control treatment, only unscented water was injected into the tank. A set of 21 fish took part in the two treatment trials and a different set of 21 fish took part in the two control trials. Horizontal lines represent the median, boxes indicate interquartile ranges and vertical lines show the range excluding outliers (circles).





**Figure 5.** The number of times pairs of fish were found within one body length from each other after exiting the bottle (maximum = 24). Horizontal lines represent the median, boxes indicate interquartile ranges and vertical lines show the range excluding outliers (circles).

Acquiring information about the environment is critical for the survival of animals (Galef & Laland, 2005) and social interactions allow animals to acquire this information rapidly and efficiently (Laland & Williams, 1997). Guppies are known to associate with other species in Trinidad (Camacho-Cervantes, Ojanguren, et al., 2014) and also in Mexico (Camacho-Cervantes, Macías-García, et al., 2014), where they are invasive. However, in the invasive context, guppies were more likely to associate with the species that had a more closely matched shoaling behaviour (Camacho-Cervantes, Macías-García, et al., 2014).

Fitness in sociable species is linked to group size and group dynamics (Cote, Fogarty, & Sih, 2012). Fish find food sources by sampling and observing other fish (Warburton, 2003) and sometimes copying them (Laland, 2008). Attraction to a particular location because of the presence or success of other species has been demonstrated experimentally in the field for many taxa (Avargues-Weber, Dawson, & Chittka, 2013; Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Monkkonen & Forsman, 2002; Seppanen, Forsman, Monkkonen, & Thomson, 2007; Seppanen & Forsman, 2007). Acquiring knowledge from other species may have a significant effect on adaptation to new environmental conditions and thus on the spread and success of populations (Loukola, Seppanen, Krams, Torvinen, & Forsman, 2013; Seppanen et al., 2007). In species that gain fitness benefits from being social, foraging information may be transmitted between individuals by processes as simple as following (Laland & Williams, 1997). This mechanism could be involved in our transmission of information experiment, i.e. guppies might be changing their swimming pattern as a response to their tendency to shoal with the informants. Other benefits of being part of a larger group can include predator avoidance and more effective evasion of attacks.

In our exploratory behaviour experiment, focal guppies engaged in exploratory behaviour more readily when in an environment with plants and were more willing to associate with the given shoaling partner in the environment without plants, regardless of the species of the second fish. Moreover, there was no difference in the species of the first fish to engage in exploratory behaviour when the pairs were composed of one guppy and one butterfly splitfin, nor in the difference in time between the first and the second fish to exit the refuge. These results are consistent with the concept of

common interests (Leimar & Hammerstein, 2010), i.e. individuals may decide to remain together when the interaction is beneficial for both (Dugatkin, 1997; Milinski, 1996).

Access to information about food sources or refuges from predators may be a key factor determining an individual's fitness (Bshary & Bergmueller, 2008). Thus, if the group is composed of more than one species but all the members benefit, they will choose to remain together. In our study, individuals were more likely to remain together when exploring an environment without plants. Potentially, they would benefit equally, even if they were not the same species, from exiting the refuge and remaining together in an open environment (like the one presented here). Moreover, we found that individuals began exploratory behaviour earlier when the novel environment had plants in it. As with the tendency to remain together, we consider complex environments to provide shelter and protection from predators (Orpwood, Magurran, Armstrong, & Griffiths, 2008). In general we found that guppies behaved similarly when paired with a conspecific or a heterospecific; however, we cannot conclude that they are keener to explore an unknown habitat when paired with a heterospecific than when alone as this lies outside the scope of our study.

Guppies associate with heterospecific individuals even when they have not encountered the species before (Camacho-Cervantes, Ojanguren, et al., 2014). Here we have shown that guppies can access information from a species of goodeid, *A. splendens*, and are willing to explore an unknown environment with them. Our results suggest that sociability in guppies is a trait that has advantages during the first stages of invasion, particularly if conspecifics are scarce.

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