

Research Article

Foraging behaviour of a native topminnow when shoaling with invaders

Morelia Camacho-Cervantes¹, Vianey Palomera-Hernandez¹ and Constantino Macías García^{2,*}¹Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510, Mexico City, Mexico²Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510, Mexico City, MexicoAuthor e-mails: mcc@cmarl.unam.mx (MCC), vipalher@gmail.com (VPH), maciasg@unam.mx (CMG)

*Corresponding author

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Abstract

Individuals join a group when the benefits of doing so outweigh the disadvantages. Typically, groups are composed by individuals of the same species, as sharing the benefits with relatives dilutes the disadvantages of being part of a group. However, mixed species shoals do occur in the wild. The Mexican Goodeidae are a clade of viviparous topminnows endemic to Central Mexico. Survival of most species is under threat, with some already extinct in nature. Causes of decline include the introduction of exotic species. These include viviparous topminnows of the Family Poeciliidae, such as the Trinidadian guppy (*Poecilia reticulata* Peters, 1859), as well as the twospot- (*Pseudoxiphophorus bimaculatus* Heckel, 1848) and porthole livebearer (*Poeciliopsis gracilis* Heckel, 1848), both native to the Mexican coastal slopes but frequently translocated to the central Highlands. Guppies and goodeids readily associate with each other, and guppies entering such associations improve their foraging efficiency. This has been hailed as evidence of a social skill that favours the establishment of viable guppy populations across the globe. It is as yet unknown whether this improvement in guppy foraging efficiency comes at a cost for the interacting goodeids. Here, we investigated how sharing resources with poeciliid invaders affects the foraging efficiency of the goodeid twoline skiffia (*Skiffia bilineata* Bean, 1887). We measured the time it took them to locate food and the total time spent eating when part of a mixed species shoal that included either a species of exotic poeciliids (guppies, twospot- or porthole livebearers), or another goodeid (*Goodea atripinnis*). We also measured foraging efficiency of twoline Skiffia in single-species (conspecific) shoals as a control. We found that the total foraging time of twoline skiffias is reduced when shoaling with guppies and twospot livebearers compared to when associating with conspecifics. We provide evidence to support the idea that native species' fitness is reduced when invaders with similar ecological requirements occupy their habitats.

Key words: sociability, invasive species, freshwater, fish, heterospecific interactions

Introduction

In the wild, animals perform the majority of their vital tasks in groups (e.g., avoiding predators, foraging, mating), but the benefits of group living can also come at a cost for its members (Krause and Ruxton 2002). For example, when living in groups, individuals have to share resources with group members, or can acquire parasites from others (Piyapong 2012;

Gavrilov 2014). Thus, the decision of which group to associate with directly affects an individual's fitness.

Usually, social interactions occur in single-species groups (Krause and Ruxton 2002), yet mixed species associations are not uncommon in nature. Examples include fishes, mammals, birds and others (Ward et al. 2002; Stensland et al. 2003; Camacho-Cervantes et al. 2014b, 2018; Farine et al. 2014). Individuals associate with others, even of different species, when the benefits of doing so outweigh the disadvantages (Ward et al. 2002). For example, lesser kestrels (*Falco naumanni*) and jackdaws (*Corvus monedula*) nest in close vicinity to decrease the energy they spend in scanning for predators (Campobello et al. 2012). Amongst fishes, killifish (*Fundulus heteroclitus* and *F. diaphanus*) associate with golden shiners (*Notemigonus crysoleucas*), white suckers (*Catostomus commersoni*) and sticklebacks (*Gasterosteus aculeatus* and *Apeltes quadracus*) to enhance the confusion effect and benefit from early predator warnings (Krause et al. 2005).

Sociability may influence several activities, and this is particularly true in the case of foraging. Factors that influence the acquisition and assimilation of food can have significant consequences for the condition, growth, survival and recruitment of individuals (Nunn et al. 2012). Foraging in groups can enhance efficiency, as being part of a group can, for example, reduce the time it takes for an individual to locate food (Day et al. 2001; van der Post and Semmann 2011; Camacho-Cervantes et al. 2014a). One mechanism involves cues that are provided, intentionally or otherwise, by foraging individuals, and that can be perceived by con- or heterospecifics to detect and exploit food. For example, some fish species will exploit public information if their personal information about a food patch is unreliable or out-dated (Kendal et al. 2009), or will use the same route as other individuals even if it is longer and more energetically costly than alternative routes (Laland and Williams 1997). Foraging in groups may also entail some costs, as individuals that forage with others can experience enhanced competition for food, time-wasting social interactions, etc. (Gavrilov 2014; Kazahari 2014; Valero et al. 2005). When foraging with other species, these disadvantages may be even greater. Fishes, for example, may alter their diets, and have lower growth rates in the presence of other species (Ward et al. 2002).

Invasive species are amongst the greatest threats to biodiversity (Pejchar and Mooney 2009; Ehrenfeld 2010; Tittensor et al. 2014; Hulme and Le Roux 2016). Invaders tend to arrive in novel environments in small groups of only a few individuals (Mack et al. 2000). For social invasive species, this represents a challenge as they may be subject to Allee effects – the disadvantages of being part of a small group (Courchamp et al. 2008; Tobin et al. 2011). Still, once invaders manage to establish they are known to interfere with the behaviour of native species (Bleach et al. 2015).

Outcomes of biological invasions are often subtle, but they can be severe, inducing native species to adapt within a few generations in response to invasions (Stuart et al. 2014).

The invasive guppy (*Poecilia reticulata*), a Trinidadian topminnow that has established populations in over 70 countries around the globe (Deacon et al. 2011), is believed to overcome some of the disadvantages of being part of a small group by associating with local species, as evidenced by their interactions with the native Mexican topminnow clade Goodeinae (Camacho-Cervantes et al. 2014a, 2015). The Goodeinae clade is composed of *ca.* 45 species and they are declining in the wild, a trend linked to the presence of exotic fish species including guppies and other poeciliids (Webb et al. 2004; Dominguez-Dominguez et al. 2008; Magurran 2009; Gesundheit and Macías Garcia 2018). The similar diets, foraging behaviour and ecological requirements of invasive poeciliids and goodeids allow poeciliids to benefit from their association, but whether it poses a disadvantage for goodeids has never been tested.

The main goal of our experiment was to determine whether shoaling with invasive species could affect foraging efficiency of native Mexican topminnows. We used the twoline skiffia (*Skiffia bilineata*) as our focal species, and, as invasive shoaling partners, the guppy and two other poeciliids reported to be present in the Mexican Central Plateau: the twospot livebearer, *Pseudoxiphophorus bimaculatus*, which was translocated from the Atlantic slope and competes with goodeids (Ramírez Carrillo and Macías Garcia 2014), and the porthole livebearer, *Poeciliopsis gracilis*, which was also translocated to the High Plateau from the lowlands of the Atlantic slope. Additionally, we included a treatment using another goodeid as shoaling companion, the blackfin goodea (*Goodea atripinnis* Jordan, 1880) and a conspecific treatment as a control.

Materials and methods

Experiments were carried out in the Instituto de Ecología of the Universidad Nacional Autónoma de México (UNAM) in Mexico City during June 2018. Sixty female twoline skiffia and 60 female blackfin goodea were collected from stock populations kept in outdoor ponds at the Instituto de Ecología UNAM. Invasive poeciliid species (100 fish per species) were collected using minnow traps and hand nets in the Tula River at Mixquiahuala (20°30'25"N; 99°14'44"W). After collection, all fish were carefully transported in plastic 2 L containers half filled with water and half filled with air, and placed in 40 L stock tanks in the aquarium of the Instituto de Ecología. A maximum of 15 fish were kept in each single-species stock tank. Fish were allowed to habituate to the aquarium for two weeks during which they received preventive medication and their health was regularly monitored. No fish showed symptoms of disease. Tanks were

Table 1. Treatments. Mixed species shoals contained the focal fish plus another twoline skiffia and two individuals of another species.

Shoal	Twoline skiffias	Other species
Single species	Focal + 3	–
With blackfin goodeids	Focal + 1	2
With guppies	Focal + 1	2
With twospot livebearers	Focal + 1	2
With porthole livebearers	Focal + 1	2

set up with aged tap water, which was treated with Stress Coat® in order to reduce stress in fish by providing them with a skin coating that replaces the one they may have lost through handling. Each tank contained a foam filter activated by an air pump and aquatic moss. Fish were maintained under a 12L:12D photoperiod. Daily water temperature ranged between 19 °C and 22 °C. Tanks were visually isolated from one another by placing a sheet of acrylic between them. Individuals to be used as focal fish during observations were kept separate from individuals to be used as shoal members for at least two weeks prior to observations to avoid familiarity effects (Griffiths and Magurran 1997). Fish were fed with commercial flake food daily but were food deprived for 12 hr prior to beginning observations.

Given that female fish allocate more time to shoaling and foraging than males, and to avoid sexually motivated behaviour, we used only female fish in our experiment. We set up an observation tank (50 × 35 × 35 cm) that contained only a sunken flake in a corner. This sunken flake was a ~ 1 cm² food flake selected from the flakes container, it was introduced in the tank and it sunk once wet. The flake was then moved to a corner; the corner used for each observation was randomized to avoid bias. Fish were already familiarized with flakes as they had been fed with them in the aquarium for two weeks prior to observations. Any portion of the flake that was not consumed was removed after the trial. We quantified the foraging behaviour of a focal twoline skiffia with different shoal compositions (Table 1).

We used a repeated measures approach in which twoline skiffia females were selected prior to the start of the observations, and were observed five times in total, once per day, with a different shoal composition each day. Shoal members were randomly selected from three stock tanks of each species to avoid pseudoreplication (Hurlbert 1984). Treatments were presented to each focal fish in a random order during the week. Observations were made between 9:00 and 13:00 h by a single observer. In total, we performed 20 replicates. Focal fish were kept in individual tanks (3 L) only during their observation week; they were allowed to see other fish in adjacent tanks to avoid stress due to social deprivation. After finishing the observations, focal fish were transferred to a stock tank and were not re-used in this experiment. All focal fish and shoals presented to them were photographed to measure their standard length (SL) in order to verify the absence of size effects on behaviour.

At the beginning of the trial the focal fish and shoaling partners were kept in a perforated 8 cm diameter bottle for at least 10 min to acclimatize while preventing them from exploring the tank until the observation began, which was when the shoal was gently released by lifting the bottle. As 10 minutes is sufficient to quantify foraging behaviour in similar experimental conditions (Camacho-Cervantes et al. 2014a), focal fish and shoal were observed for 10 min to determine: the time and species of the first fish to locate the food (the exact second when the first fish started consuming food), the time it took the focal fish to locate the food (exact second it started consuming food); the time the focal fish spent foraging (number of seconds spent consuming food); the number of focal fish foraging periods (times the focal fish approached the food and consumed it); and any aggressive interaction directed to the focal fish (bites from other fish). Total foraging time of the focal fish was analysed using the fraction of time spent foraging from the available time.

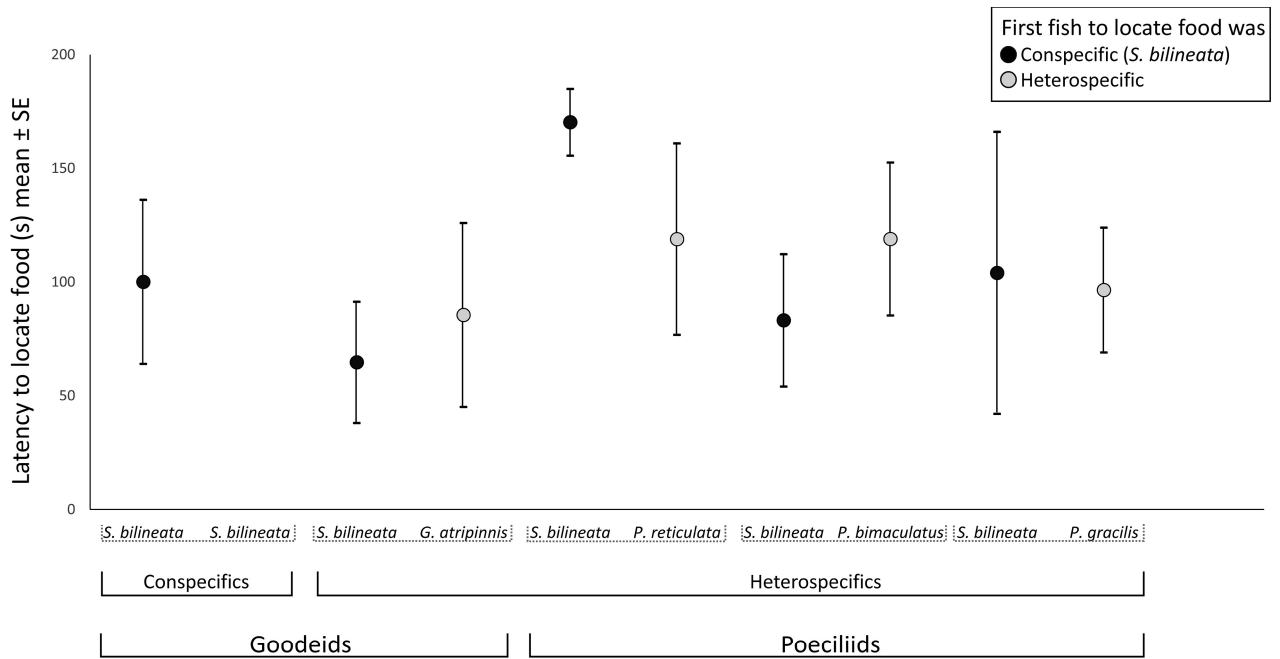
Statistical analyses

Fish used during this experiment were selected to be around the same size (average SL = 33.7 mm, SD = 6.3 mm), the difference in size between the focal fish and the shoal was similar in all treatments (ANOVA: $F_{4,100} = 1.325$, $p = 0.266$). There was no relation between the size of the focal fish relative to that of the shoal and the time it took it to locate food ($R^2 = -0.011$) or the time it spent eating during the observations ($R^2 = -0.001$). Therefore, size was removed from the analyses. There was no aggression recorded during any of the observations, thus it was not possible to analyse this variable.

We used X^2 tests to compare the number of times that the first fish to locate the food was a twoline skiffia or a heterospecific. To compare the time it took the focal twoline skiffia to locate food and the time it spent foraging among the different treatments, we used linear mixed effects models (lme). Given that our study uses a repeated measures approach our random factor for the analysis was the identification number of each focal twoline skiffia (Pinheiro et al. 2013). We included in the comparison the time it took the first fish to locate food and the time it took the focal fish to locate it. This comparison provides a measure of the efficiency with which the focal fish acquired information from other fish about the location of food; consequently, we excluded from the analyses all the cases where the first fish to locate food was the focal fish. *A posteriori* Tukey HSD tests (glht) were carried out to identify which treatments were different (Genz et al. 2013). All analyses were carried out with R (R Core Team 2018).

Ethical note

Data collected for the purposes of this experiment were purely observational. No fish used in this experiment died. After the experiment was completed



Feeding performance of *Skiffia bilineata* in the presence of

Figure 1. Latency (mean ± SE) in seconds for the focal fish to locate the food once it had been initially located by another fish (max = 600 s). Focal twoline skiffia (*Skiffia bilineata*) were observed in single species groups of conspecifics, or in mixed species groups (Heterospecific groups). The latter were formed of twoline skiffia and 1) another species form the same family (the Goodeid *Goodea atripinnis*) or 2) Poeciliid fish belonging to one of the following species; Trinidadian guppy (*Poecilia reticulata*), Twoline livebearer (*Pseudoxiphophorus bimaculatus*) and porthole livebearer (*Poeciliopsis gracilis*). ● = replicates in which food was first located by a twoline skiffia that was not the focal fish; ○ = replicates where the first to locate the food was a heterospecific.

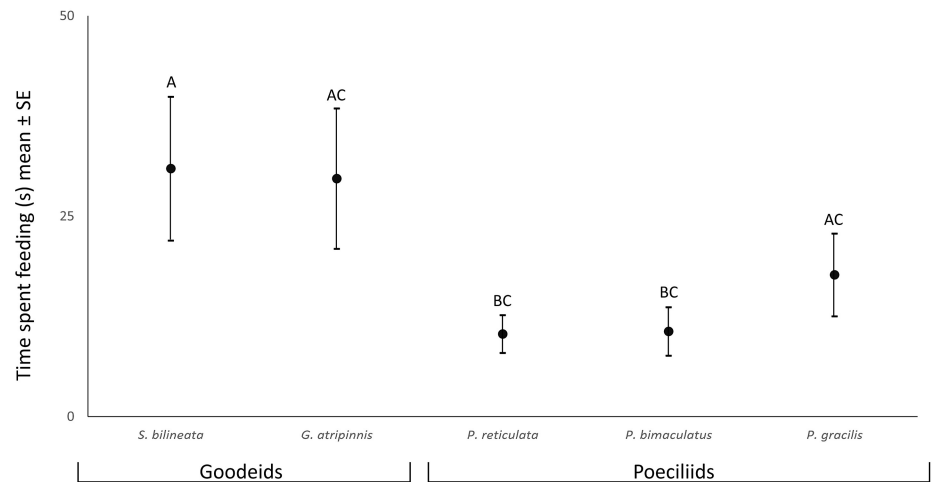
(30 days), all fish remained in stock tanks at the Instituto de Ecología aquarium to be used in future experiments.

Results

In sixteen out of the 20 replicates, guppies located food before twoline skiffias ($X^2_1 = 7.2$, $p = 0.007$). In the three remaining mixed species shoal treatments, twoline skiffias located food approximately as often as the other species did ($X^2_1 = 3.2$, $p = 0.073$). We found no differences in the time it took the focal fish to locate food regardless of the composition of the shoal (lme: $F_{4,100} = 0.926$, $p = 0.454$).

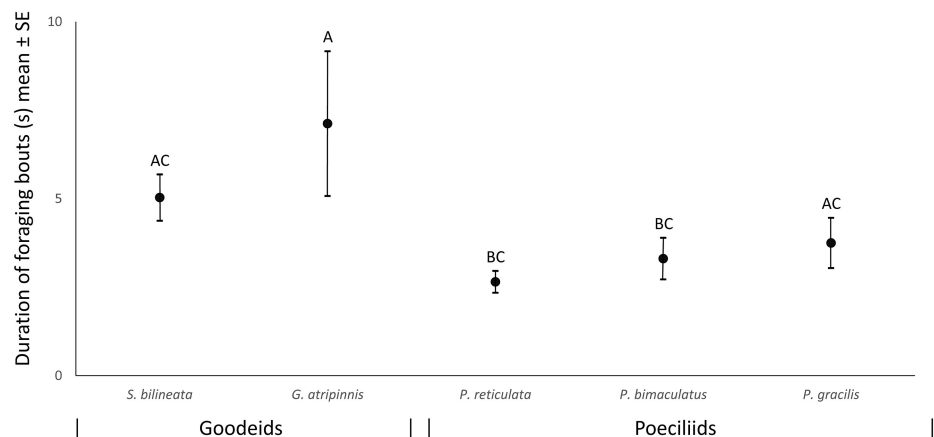
In observations where the focal fish was not the first to find the food (68 out of the total 100), neither the treatment (lme: $F_{4,68} = 0.517$, $p = 0.723$; Figure 1), nor the identity of the first fish to locate food (heterospecific or conspecific), had an effect on the time focal fish took to locate food after the first fish found it (lme: $F_{1,68} = 0.107$, $p = 0.745$; Figure 1).

The total amount of time that focal twoline skiffias spent eating was different among treatments (lme: $F_{4,100} = 3.15$, $p = 0.019$; Figure 2). A Tukey post-hoc analysis revealed that twoline skiffias spent less time eating when accompanied by guppies ($Z = 2.588$, $p = 0.07$) and twospot livebearers ($Z = 2.548$, $p = 0.08$). We found no difference between the number of foraging bouts made by the focal fish when accompanied by the different species tested (lme: $F_{4,100} = 0.724$, $p = 0.578$).



Feeding performance of focal *Skiffia bilineata* in the presence of

Figure 2. Total time (mean ± SE) in seconds devoted by focal fish to eat (max = 600 s). Letters represent differences between treatments: treatments that do not share a letter are significantly different.



Feeding performance of focal *Skiffia bilineata* in the presence of

Figure 3. Duration (mean ± SE) of foraging bouts in seconds was different among treatments (max = 600 s). Treatments not sharing a letter are significantly different.

Duration of foraging bouts was different among treatments (lme: $F_{4,100} = 3.311$, $p = 0.016$; Figure 3). A Tukey post-hoc analysis revealed that the foraging periods of focal fish when housed with blackfin goodea (a relative that is naturally sympatric with *S. bilineata*) were longer than when sharing the tank with the exotic guppies ($Z = 3.235$, $p = 0.011$) or twospot livebearers ($Z = 2.782$, $p = 0.043$).

Discussion

We assessed the foraging efficiency of an endangered Goodeid fish, the twoline skiffia (*S. bilineata*), in the presence of potential competitors from its own species only (conspecifics) or from their own and another species (heterospecifics). We found no effect of shoal composition on the speed with which twoline skiffia found food. We did find, however, that twoline

skiffia performed better, in terms of duration of feeding bouts and total time spent feeding, when foraging in conspecific shoals, or in the company of its close relative, the sympatric blackfin goodea, than in shoals with a poeciliid species. In particular, the feeding performance of twoline skiffia was worst when shoaling with guppies (*P. bilineata*), and with the twospot livebearer (*P. bimaculatus*). Compared to twoline skiffias, guppies were the most efficient at locating food.

The Mexican Central Plateau is already inhabited by the three poeciliid species used in this experiment. Guppies were already suspected to decrease the fitness of female goodeids that they sexually harass (Valero et al. 2008). Our experiment shows that sociability between native twoline skiffias and invasive poeciliids also causes damage to goodeids by reducing the time they can allocate to foraging activities. This is a further possible mechanism to explain the decrease of goodeid populations following poeciliid invasions (Magurran 2009). The effect of twospot livebearer on twoline skiffias foraging aligns with the findings of Ramírez Carrillo and Macías Garcia (2014) that foraging and aggressive interference of this translocated fish can potentiate the negative effects of global warming on the high-plateau population of the darkedged splitfin goodeid (*Girardinichthys multiradiatus*).

In terms of competition for resources, the threat posed by invaders is directly proportional to how much they share ecological requirements with native species (Cini et al. 2018). Indeed, competition is suggested as one of the main drivers for native species fitness reduction (Strayer et al. 2006). Invaders may outcompete natives directly, by depleting common resources and forcing native organisms to rely on sub-optimal ones (Bohn and Amundsen 2001), or indirectly, by interfering with natives' access to resources (Warnock and Rasmussen 2013). The mechanisms behind the reduction of twoline skiffias foraging efficiency when shoaling with invaders are yet to be explored. Given that food in our experiment was in plentiful supply, we hypothesise that the reason behind twoline skiffia's decreased foraging time is linked to interference competition. Interference has also been strongly implied in the interaction between the amarillo fish (also known as blackedged splitfin) and the twospot livebearer. Following the introduction of the latter—a lowland species—to a temperate mountain lake, the native amarillo experienced a shift in its reproductive season towards the colder winter months, when the invasive poeciliid population is at its lowest. Native amarillo fish in a nearby lake (ca. 0.5 km apart), which remains free of the invasive, continue to breed from spring to autumn (Ramírez Carrillo and Macías Garcia 2014). Examples of competitive interference of invasive on native species are not limited to fish, and are common in other taxa; e.g. invasive parakeets negatively impact native species foraging behaviour simply by being present in the vicinity of natives' potential resources (Peck et al. 2014).

Previous research on guppies suggest that in Mexico they have already been able to gain benefits from heterospecific shoaling with natives. Guppies are able to acquire information and to forage for longer periods when associating with natives than when being in smaller conspecific groups (Camacho-Cervantes et al. 2014a). Also, they can obtain information on food availability and gain other benefits linked to exploratory behaviour such as an increase in boldness when accompanied by natives (Camacho-Cervantes et al. 2015). Limited research has been carried out on the mechanisms through which twospot livebearers have been able to establish themselves in central Mexico. Being a social species, these fish too might be subject to Allee effects during the first stages of invasions. Twospot livebearers are larger and more aggressive than guppies, and share various ecological requirements with goodeids (Ramírez Carrillo and Macías Garcia 2014), thus, in addition to benefiting from social skills displayed by guppies, it may aggressively displace native goodeids. We note that in our experiment, only guppies were faster than twoline skiffias at locating food. Further research must be carried out on the behaviour of twospot and porthole livebearers as their invasive populations are increasing in the wild. However, we found no evidence that these species outcompeted twoline skiffias by being quicker to find food or reducing their foraging efficiency. Guppies, porthole livebearers and twospot livebearer are similar; they have similar ecological requirements, are roughly in the same size range, and are social species. Nevertheless guppies were the only species that showed signs of being quicker to locate food in comparison to twoline skiffias.

In the case of goodeids and guppies, research suggests that both taxa could benefit during an initial period, but that competition between them may subsequently be a disadvantage for natives (Chivers et al. 2002; Ward et al. 2002; Camacho-Cervantes et al. 2018). Guppies and twoline skiffias are both social and prefer to join a shoal rather than remaining alone, but guppies show a higher tendency to associate with conspecifics while twoline skiffias have the same tendency to join a conspecific or an heterospecific shoal (Camacho-Cervantes et al. 2018). The later suggests that after the initial invasion stage, when guppies become more abundant they would associate with themselves rather than join heterospecific shoals and would possibly outcompete natives. Our results provide evidence to support this in a foraging scenario. There might be other interactions that may be detrimental to native goodeids that are yet to be explored. A study conducted by Dame and Petren (2006) on the invasion of the house gecko (*Hemidactylus frenatus*) in a Pacific island found that resource competition was unlikely to be the mechanism through which this gecko is displacing native ones. Rather, they point at sexual interference as a possible cause, and we know that, while inconsequential in terms of generating hybrids, poeciliids do interfere sexually with goodeids (Valero et al. 2008).

Invasive species are often superior competitors in relation to populations of native species that have not experienced their competition over evolutionary time (Piria et al. 2017). We now have evidence that foraging efficiency of native goodeids is impaired by the presence of invasive poeciliids, and must now investigate what the consequences of this interference may be in terms of fitness and demography. Indeed, the study of impacts of invading species—including impacts on foraging behaviour (Nunn et al. 2012)—and research on the mechanisms underlying these, are fundamental to conservation of endangered species (Cattau et al. 2016).

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References

- Bleach IT, Beckmann C, Both C, Brown GP, Shine R (2015) Noisy neighbours at the frog pond: effects of invasive cane toads on the calling behaviour of native Australian frogs. *Behavioral Ecology and Sociobiology* 69: 675–683, <https://doi.org/10.1007/s00265-015-1879-z>
- Bohn T, Amundsen PA (2001) The competitive edge of an invading specialist. *Ecology* 82: 2150–2163, [https://doi.org/10.1890/0012-9658\(2001\)082\[2150:TCEOAI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2150:TCEOAI]2.0.CO;2)
- Camacho-Cervantes M, Macias Garcia C, Ojanguren AF, Magurran AE (2014a) Exotic invaders gain foraging benefits by shoaling with native fish. *Royal Society Open Science* 1: 140101, <https://doi.org/10.1098/rsos.140101>
- Camacho-Cervantes M, Ojanguren AF, Deacon AE, Ramnarine IW, Magurran AE (2014b) Association tendency and preference for heterospecifics in an invasive species. *Behaviour* 151: 769–780, <https://doi.org/10.1163/1568539X-00003169>
- Camacho-Cervantes M, Ojanguren AF, Magurran AE (2015) Exploratory behaviour and transmission of information between the invasive guppy and native Mexican topminnows. *Animal Behaviour* 106: 115–120, <https://doi.org/10.1016/j.anbehav.2015.05.012>
- Camacho-Cervantes M, Ojanguren AF, Domínguez-Domínguez O, Magurran AE (2018) Sociability between invasive guppies and native topminnows. *PLoS ONE* 13: e0192539, <https://doi.org/10.1371/journal.pone.0192539>
- Campobello D, Sara M, Hare JF (2012) Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies. *Behavioral Ecology* 23: 425–433, <https://doi.org/10.1093/beheco/arr207>
- Cattau CE, Fletcher RJ, Reichert BE, Kitchens WM (2016) Counteracting effects of a non-native prey on the demography of a native predator culminate in positive population growth. *Ecological Applications* 26: 1952–1968, <https://doi.org/10.1890/15-1020.1>
- Chivers DP, Mirza RS, Johnston JG (2002) Learned recognition of heterospecific alarm cues enhances survival during encounters with predators. *Behaviour* 139: 929–938, <https://doi.org/10.1163/156853902320387909>
- Cini A, Cappa F, Petrocelli I, Pepicciello I, Bortolotti L, Cervo R (2018) Competition between the native and the introduced hornets *Vespa crabro* and *Vespa velutina*: a comparison of potentially relevant life-history traits. *Ecological Entomology* 43: 351–362, <https://doi.org/10.1111/een.12507>
- Courchamp F, Berek L, Gascoigne J (2008) Allee effects in ecology and conservation. Oxford Scholarship Online. <https://doi.org/10.1093/acprof:oso/9780198570301.001.0001>
- Dame EA, Petren K (2006) Behavioural mechanisms of invasion and displacement in Pacific island geckos (*Hemidactylus*). *Animal Behaviour* 71: 1165–1173, <https://doi.org/10.1016/j.anbehav.2005.10.009>
- Day RL, MacDonald T, Brown C, Laland KN, Reader SM (2001) Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour* 62: 917–925, <https://doi.org/10.1006/anbe.2001.1820>
- 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>
- Dominguez-Dominguez O, Zambrano L, Escalera-Vazquez LH, Perez-Rodriguez R, Ponce de Leon GP (2008) Changes in the distribution of goodeids (Osteichthyes: Cyprinodontiformes: Goodeidae) in river basins of Central Mexico. *Revista Mexicana de Biodiversidad* 79: 501–512

- Ehrenfeld JG (2010) Ecosystem Consequences of Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics* 41: 59–80, <https://doi.org/10.1146/annurev-ecolsys-102209-144650>
- Farine DR, Downing CP, Downing PA (2014) Mixed-species associations can arise without heterospecific attraction. *Behavioral Ecology* 25: 574–581, <https://doi.org/10.1093/beheco/aru023>
- Gavrilov VV (2014) Advantages and limitations of interspecies associations in northern migratory sandpipers (Charadrii, Aves). *Zhurnal Obshchei Biologii* 75: 204–213
- Genz A, Bretz F, Miwa T, Mi X, Leisch F, Scheipl F, Bornkamp B, Maechler M, Hothorn T (2013) mvtnorm: Multivariate Normal and t Distributions. <http://CRAN.R-project.org/package=mvtnorm>
- Gesundheit P, Macías Garcia C (2018) The role of introduced species in the decline of a highly endemic fish fauna in Central Mexico. *Aquatic Conservation: Marine and Freshwater Ecosystems* 2018: 1–12, <https://doi.org/10.1002/aqc.2927>
- Griffiths SW, Magurran AE (1997) Familiarity in schooling fish: how long does it take to acquire? *Animal Behaviour* 53: 945–949, <https://doi.org/10.1006/anbe.1996.0315>
- Hulme PE, Le Roux JJ (2016) Invasive species shape evolution. *Science* 352, 422–422, <https://doi.org/10.1126/science.352.6284.422-b>
- Hurlbert SH (1984) Pseudoreplication and the Design of Ecological Field Experiments. *Ecological Monographs* 54: 187–211, <https://doi.org/10.2307/1942661>
- Kazahari N (2014) Maintaining social cohesion is a more important determinant of patch residence time than maximizing food intake rate in a group-living primate, Japanese macaque (*Macaca fuscata*). *Primates* 55: 179–184, <https://doi.org/10.1007/s10329-014-0410-x>
- Kendal JR, Rendell L, Pike TW, Laland KN (2009) Nine-spined sticklebacks deploy a hill-climbing social learning strategy. *Behavioral Ecology* 20: 238–244, <https://doi.org/10.1093/beheco/arp016>
- Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, 224 pp
- Krause J, Ward AJW, Jackson AL, Ruxton GD, James R, Currie S (2005) The influence of differential swimming speeds on composition of multi-species fish shoals. *Journal of Fish Biology* 67: 866–872, <https://doi.org/10.1111/j.0022-1112.2005.00768.x>
- Laland KN, Williams K (1997) Shoaling generates social learning of foraging information in guppies. *Animal Behaviour* 53: 1161–1169, <https://doi.org/10.1006/anbe.1996.0318>
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710, [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Magurran AE (2009) Threats to Freshwater Fish. *Science* 325: 1215–1216, <https://doi.org/10.1126/science.1177215>
- Nunn AD, Tewson LH, Cowx IG (2012) The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries* 22: 377–408, <https://doi.org/10.1007/s11160-011-9240-8>
- Peck HL, Pringle HE, Marshall HH, Owens IPF, Lord AM (2014) Experimental evidence of impacts of an invasive parakeet on foraging behavior of native birds. *Behavioral Ecology* 25: 582–590, <https://doi.org/10.1093/beheco/aru025>
- Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution* 24: 497–504, <https://doi.org/10.1016/j.tree.2009.03.016>
- Piria M, Copp GH, Dick JTA, Duplic A, Groom Q, Jelic D, Lucy FE, Roy HE, Sarat E, Simonovic P, Tomljanovic T, Tricarico E, Weinlander M, Adamek Z, Bedolf S, Coughlan NE, Davis E, Dobrzycka-Krahel A, Grgic Z, Kirankaya SG, Ekmekci FG, Lajtner J, Lukas JAY, Koutsikos N, Mennen GJ, Mitic B, Pastorino P, Ruokonen TJ, Skora ME, Smith ERC, Spren N, Tarkan AS, Treer T, Vardakas L, Vehanen T, Vilizzi L, Zanella D, Caffrey JM (2017) Tackling invasive alien species in Europe II: threats and opportunities until 2020. *Management of Biological Invasions* 8: 273–286, <https://doi.org/10.3391/mbi.2017.8.3.02>
- Piyapong C (2012) Shoaling and Factors Underlying Shoal Composition in Fish. *KKU Science Journal* 40(4): 1002–1012
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Ramírez Carrillo E, Macías Garcia C (2014) Limited options for native goodeid fish simultaneously confronted to climate change and biological invasions. *Biological Invasions* 17: 245–256, <https://doi.org/10.1007/s10530-014-0723-0>
- Stensland E, Angerbjorn A, Berggren P (2003) Mixed species groups in mammals. *Mammal Review* 33: 205–223, <https://doi.org/10.1046/j.1365-2907.2003.00022.x>
- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution* 21: 645–651, <https://doi.org/10.1016/j.tree.2006.07.007>
- Stuart YE, Campbell TS, Hohenlohe PA, Reynolds RG, Revell LJ, Losos JB (2014) Rapid evolution of a native species following invasion by a congener. *Science* 346: 463–466, <https://doi.org/10.1126/science.1257008>
- Tittensor DP, Walpole M, Hill SLL, Boyce DG, Britten GL, Burgess ND, Butchart SHM, Leadley PW, Regan EC, Alkemade R, Baumung R, Bellard C, Bouwman L, Bowles-Newark NJ, Chenery AM, Cheung WWL, Christensen V, Cooper HD, Crowther AR, Dixon

- MJR, Galli A, Gaveau V, Gregory RD, Gutierrez NL, Hirsch TL, Höft R, Januchowski-Hartley SR, Karmann M, Krug CB, Leverington FJ, Loh J, Lojenga RK, Malsch K, Marques A, Morgan DHW, Mumby PJ, Newbold T, Noonan-Mooney K, Pagad SN, Parks BC, Pereira HM, Robertson T, Rondinini C, Santini L, Scharlemann JPW, Schindler S, Sumaila UR, Teh LSL, van Kolck J, Visconti P, Ye YM (2014) A mid-term analysis of progress toward international biodiversity targets. *Science* 346: 241–244, <https://doi.org/10.1126/science.1257484>
- Tobin PC, Berec L, Liebhold AM (2011) Exploiting Allee effects for managing biological invasions. *Ecology Letters* 14: 615–624, <https://doi.org/10.1111/j.1461-0248.2011.01614.x>
- Valero A, Hudson R, Luna EÁ, Macías Garcia C (2005) A cost worth paying: Energetically expensive interactions with males protect females from intrasexual aggression. *Behavioral Ecology and Sociobiology* 59: 262–269, <https://doi.org/10.1007/s00265-005-0033-8>
- Valero A, Macías Garcia C, Magurran AE (2008) Heterospecific harassment of native endangered fishes by invasive guppies in Mexico. *Biology Letters* 4: 149–152, <https://doi.org/10.1098/rsbl.2007.0604>
- van der Post DJ, Semmann D (2011) Patch depletion, niche structuring and the evolution of cooperative foraging. *BMC Evolutionary Biology* 11: 335, <https://doi.org/10.1186/1471-2148-11-335>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R-Core-Team (2013) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-1092013
- Ward AJW, Axford S, Krause J (2002) Mixed-species shoaling in fish: the sensory mechanisms and costs of shoal choice. *Behavioral Ecology and Sociobiology* 52: 182–187, <https://doi.org/10.1007/s00265-002-0505-z>
- Warnock WG, Rasmussen JB (2013) Assessing the effects of fish density, habitat complexity, and current velocity on interference competition between bull trout (*Salvelinus confluentus*) and brook trout (*Salvelinus fontinalis*) in an artificial stream. *Canadian Journal of Zoology* 91: 619–625, <https://doi.org/10.1139/cjz-2013-0044>
- Webb SA, Graves JA, Macias Garcia C, Magurran AE, Ófoighil D, Ritchie MG (2004) Molecular phylogeny of the livebearing Goodeidae (Cyprinodontiformes). *Molecular Phylogenetics and Evolution* 30: 527–544, [https://doi.org/10.1016/S1055-7903\(03\)00257-4](https://doi.org/10.1016/S1055-7903(03)00257-4)