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Research Article

Personality-dependent survival of the invasive mosquitofish: being social can be deadlyTomas Brodin^{1,2,*}, Sean Fogarty¹, Andrew Sih¹ and Julien Cote^{1,3,4}¹Department of Environmental Science and Policy, University of California, Davis, USA²Department of Wildlife, Fish and Environmental Studies, SLU - Umeå, Umeå, Sweden³CNRS, Université Paul Sabatier, ENFA, UMR5174EDB (Laboratoire Évolution & Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse, France⁴Université de Toulouse, UMR5174 EDB, F-31062 Toulouse, FranceAuthor e-mails: tomas.brodin@slu.se (TB), spfogarty@gmail.com (SF), asih@ucdavis.edu (AS), julien.cote@univ-tlse3.fr (JC)

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Abstract

Mosquitofish (*Gambusia affinis*) are a widespread, invasive species that frequently colonize habitats where they might encounter novel predators. Earlier work showed that asocial mosquitofish disperse more readily than social fish. Initial colonists to newly invaded, low density sites should thus be relatively asocial. Here, we tested the hypothesis that asocial mosquitofish should survive better than social fish when exposed to predators at low mosquitofish density. We used standardized behavioural assays to quantify the individual behavioral type (boldness, sociability, activity, exploratory tendency) of 224 mosquitofish, and then exposed them to predators in small groups. As predicted, asocial individuals survived exposure to predators better than social individuals. In addition, while body mass *per se* did not affect survival, males survived predators better than females. Overall, this study provides an early corroboration of the general prediction that behavioural types that disperse more readily might also be better at coping with predators at low density.

Key words: personality traits, social tendency, invasion, predation, boldness, selection gradient

Introduction

In many species, individuals exhibit relatively stable, consistent differences in behaviour across multiple contexts where some individuals are consistently bolder, more aggressive or social than others (Sih et al. 2004). Such consistent individual differences in behaviour are referred to as behavioural types (BTs) (aka animal personality; temperaments or behavioural syndromes; Dall et al. 2004; Sih et al. 2004; Reale et al. 2007; Sih and Bell 2008).

Differences between individuals in BT are ecologically and evolutionarily important because of their effects on fitness or components of fitness (Smith and Blumstein 2008; Wolf and Weissing 2012; Sih et al. 2012). In particular, bolder, more active or aggressive animals often feed and grow at higher rates, but also take more risks and thus suffer higher mortality, in

particular, from predators (Sih et al. 2003; Brodin and Johansson 2004; Biro and Stamps 2008). Another important behavioural trait affecting fitness is sociability. Sociability refers to an individual's tendency to associate with conspecifics in a non-aggressive matter (Conrad et al. 2011). Social individuals are thus more likely than less social (hereafter referred to as asocial) individuals to be: 1) a member of a group as opposed to being alone (Cote et al. 2010a); 2) in larger as opposed to smaller groups; and 3) in more compactly-organized, cohesive groups as opposed to loosely organized groups. Accordingly, social individuals are more likely than asocial ones to gain the benefits of group living (e.g., safety in numbers (Krause and Ruxton 2002) but also to suffer the costs of group living (e.g., higher competition, detection by predators). All these behavioural types are therefore predicted to influence survival from predation. One area where BT-dependent predation might be especially important is biological invasions. When individuals of an invasive species are dispersing in a novel environment, dispersers might be naive both to the predator community and the structural complexity (e.g. natural refuges) of the invaded patch and hence might not know what to avoid and how to avoid it. We could expect the success of an invasive species to depend on whether individuals leading an invasion front are better at surviving in the presence of novel predators when compared to resident individuals, as the likelihood of encountering a novel predator should be higher at an invasion front. Indeed, the above reasoning suggests a correlation between behavioral drivers of dispersal and predator avoidance. Specifically, the hypothesis is that the BTs that are more likely to disperse should also be better than others at coping with predators.

Mosquitofish (*Gambusia* sp.) are invasive species that have been introduced for mosquito-control worldwide and have spread successfully to over 40 countries (Welcomme 1992). Their invasion success and negative impacts on native communities (Lloyd et al. 1986; Courtenay and Meffe 1989; Gamradt and Kats 1996; Webb and Joss 1997; Goodsell and Kats 1999) have earned them a place among the 100 worst invasive species worldwide (ISSG 2000). Earlier we used the same individuals as studied here to show that individual behavioural type and BT-dependent dispersal— asocial individuals generally disperse more (Cote et al. 2010a, 2011)— of the invasive mosquitofish (*Gambusia affinis*) can be consistent over long periods of time, at least 4 months (Cote et al. 2011) and can influence ecological impacts (Cote et al. 2017). Here we present results from a follow-up experiment where we test whether individual survival is BT-dependent. We used a low-density context to simulate conditions encountered in invaded areas. In particular, we test the *a priori* hypothesis that asocial and/or bold individuals, that tend to disperse readily and thus colonize new habitats at low density, also survive better than other BTs when exposed to predators. We also examine whether survival with predators is

influenced by fish body mass and sex. These results allowed us to explore patterns of selection on behaviors (directional, stabilizing, disruptive and correlational) and to provide estimates of the selection gradient.

Materials and methods

Mosquitofish (*Gambusia affinis*) were transported from the Sacramento-Yolo Mosquito and Vector Control District to the Center for Aquatic Biology and Aquaculture (CABA), University of California, Davis on August 15th 2008. Fish were held in groups of 60 in 80-L flow-through fibreglass tanks on a natural photoperiod (L/D = 14/10) at 22 °C, and fed Tetramin flakes ad libitum. Two hundred twenty-four mosquitofish were acclimated to these conditions for > 18 days prior to behavioural observations that were carried out between September 3rd and September 10th 2008 and between October 15th and October 25th 2008. These fish are part of the 463 fish used by Cote et al. (2011, 2017). At least two weeks before behavioural observations began individual mosquitofish were marked with an elastomer tag (Northwest Marine Technologies, Shaw Island, WA, USA) under a low dose (5 mg. L⁻¹) of anaesthetic (MS-222). Each fish received a randomly assigned unique identifier by injecting one of four colours (yellow, orange, blue or red) subcutaneously into 4 locations on the caudal peduncle (2 on each side). Fish were allowed to recover from anesthesia in an opaque bucket before being transferred back to their home aquaria where they were allowed to recover for at least 3 days. No differences in mortality rate were observed between marked and unmarked fish (marked fish: 2.5% over 2 days; unmarked fish: 2.7% over the same 2 days) and we checked for normal behaviour after marking by observing that behaviour was similar between sets of unmarked and marked fish (Cote et al. 2010a). One night before behavioural observations began mosquitofish were placed individually in 37.9 L aquaria, with 30 L of well-water, a 12 cm piece of 5 cm diameter PVC pipe that served as refuge, and an airstone. Ten females and 4 males per day were run through behavioural assays over 4 × 4 days. This sex-ratio matched the sex-ratio of the fish collected from the Vector Control District. To characterize BT, we ran two behavioural assays separated by one hour. First, we characterized sociability as a tendency to shoal. Second, we characterized boldness as the latency to exit from a refuge into a novel environment, and exploratory behaviour and activity as movement in a novel environment. Following the behavioural trials we performed a 24-hour predation assay.

Tendency to shoal (sociability)

We recorded the amount of time spent near a shoal of conspecifics (Ward et al. 2004). The experimental arena was an aquarium (30 cm high × 25 cm wide × 50 cm long) filled to a depth of 13.6 cm with 17 l of well-water and

divided lengthwise into three compartments (two small and one large centre compartment) using two transparent glass partitions 12.5 cm away from each side wall. The partitions allowed visual, but not physical or olfactory, interaction between the shoal and the focal individual. One of 6 predetermined stimulus shoals comprised of 14 mosquitofish was introduced to one of the smaller compartments at least 1 h before the experiments began while the other small compartment was left empty as a control. After 1 h, the first focal fish was introduced into the centre of the larger compartment and allowed to acclimate for 10 min. Black curtains surrounded the aquarium with a small slit that allowed us to observe fish without disturbing them. The position of the focal fish was then continuously recorded for 10 min using software for tracking behaviour (Observer 2.01). The large compartment was divided with vertical marks every 2 cm; time spent shoaling was defined as time spent by the focal fish within the 2 cm closest to the stimulus shoal (Cote et al. 2010a). When the assay was complete, individuals were returned to their individual home aquarium and water was changed in the centre compartment of the sociability arena to exclude confounding effects on sociability by accumulation of conspecific chemical cues in the water.

Measuring boldness and exploration in a novel environment

One hour after the sociability assay, boldness, exploration and activity levels were assessed by recording behaviour in a novel environment (Yoshida et al. 2005; Brown et al. 2007): a well lit, opaque, white plastic tank (80 cm long × 80 cm wide × 20 cm high), filled with 10 cm of well water, and furnished with half flower pots that served as additional refuges in two corners. Individual fish were added gently to an upright, cylindrical (9 cm diameter), black, opaque, covered refuge chamber placed in the opposite end from the flower pots. After 10 min, we remotely opened a 4 cm wide door on the refuge chamber, allowing fish access to the experimental arena. Black curtains surrounded the arena while cameras recorded behaviour. Trials ended either 5 min after fish left the refuge or after 45 min (2700 sec) if the fish did not leave the refuge.

Boldness was the log transformed maximum time allowed for fish to exit the refuge (log 2700 sec) minus the log latency (s) to exit the refuge and stay for > 10 consecutive seconds out of the refuge. Shorter latency to exit indicates higher boldness. Exploratory tendency was quantified by area covered (see below), and activity was measured as % time spent moving during the 5 min after the fish left the refuge.

While some have suggested that latency to emerge in a novel environment should be termed exploratory behaviour and not boldness (Reale et al. 2007), we follow several earlier papers (e.g., Yoshida et al. 2005; Brown et al. 2007; Cote et al. 2010a, 2011) in our assessment that for small, schooling

fish, a short latency to emerge alone from a dark refuge into an open, novel environment represents boldness, while exploratory tendency is measured by space use after emergence from refuge. While we would prefer independent assessments of exploration and activity, in fact, the two might not be functionally separable. To explore, animals must be active. To distinguish the two somewhat, we define activity as movement *per se*, and exploratory tendency as area covered (explored) while moving. Because the water was shallow (10 cm deep), area covered provided a useful measure of space use. Note that since these behaviours were assayed during the same trial, there may be correlated.

Videos were collected on a dedicated Micros Digital-Sprite2 DVR system and downloaded as .avi files before being exported as image stacks (1 frame per second) using Virtual-Dub. These image stacks were imported into ImageJ where the fish's position (x-y coordinates) was tracked over the five-minute assay. The % time that the fish spent moving was the % frames in which the fish moved > 1 body length in the previous second. Area explored incorporates both the distance an individual moved and the spatial pattern of those movements. Given x-y coordinates from each frame, we tracked each individual's continuous path (assuming that movements between frames were straight). Explored area was calculated (in Matlab R2007) as the percentage of the arena that fell within 5 cm of the fish's path. At the end of each observation day, mosquitofish were weighed to the nearest 0.001 g.

The individuals used here display significant rank order consistency over 4–5 months in all four behaviours assayed and these behaviours are all correlated with the exception of sociability and activity (Cote et al. 2011). We therefore performed a principal component analysis to define possible personality trait dimensions (Cote et al. 2011; for more details see Supplementary material Table S1). Hereafter, we will use three dimensions depicting sociability, boldness and exploration-activity. However, we also checked that using raw behavioural scores provided the same results (Table S6).

Predation assay

After behavioral assays were completed, fish were subjected to a dispersal assay (Cote et al. 2011) and kept in outdoors predator-free mesocosms (80 cm × 40 cm × 50 cm plastic tanks; Cote et al. 2017) for 4–5 months before predation assays began (~ 132 days). For the predation assay, 14 mosquitofish were placed in each of 4 cattle tanks (each 1.5 m diameter, filled with 40 cm of well water) providing a density of 8 fish/m². We consider this density on the low end for *G. affinis* since natural densities between 60 and 100 fish/m² are not uncommon (Mills et al. 2004; Goldsworthy and Betolli 2006). Survival in the presence of predators was assessed by exposing fish to one predatory trout (20–25 cm total length). Tanks had several forms of potential refuge

for mosquitofish: PVC tubes, flowerpots, an artificial plant and a black, plastic box (30 cm × 20 cm × 15 cm) at the bottom that mosquitofish could enter, but that excluded trout. Mosquitofish were given 1 hour to acclimate while trout were held in a screened enclosure (so mosquitofish got visual and chemical cues from trout). Trout were then released and allowed to feed for 24 hours after which we removed the trout and collected surviving mosquitofish. All surviving mosquitofish were then returned to group housing in 80-L tanks and individually identified. This procedure was repeated 4 times giving a total of 16 predation trials involving 224 mosquitofish. All mosquitofish were used in only one predation trial each.

Statistics

The sociability score for one individual and the boldness score for one individual are missing. We thus excluded these individuals from the analysis. Also, five individuals never emerged from shelter during the novel environment assay and could not be assessed for exploration/activity. As a consequence, they were excluded from the PCA (see above) and survival analyses, leaving two hundred seventeen fish to be analysed.

We analyzed survival during predation assays using a generalized linear mixed model with a logit-link, a binomial error distribution and a bobiq optimizer in R 2.13.0 and with the experimental group as a random effect (package lme4 in R 3.4.4, Bates et al. 2013). We first standardized each explanatory variable to zero mean and unit variance (Lande and Arnold 1983). We used multivariate regression to quantify linear, quadratic and correlational selection (Lande and Arnold 1983). All models included body mass and sex to control for relationship between behaviours, body mass and sex (Cote et al. 2011) and to study independent effects of behavioural dimensions. We first checked whether there was a correlational selection by including double interactions between behavioural dimensions. Second, we looked for potential disruptive or stabilizing selection by adding quadratic terms for behavioural dimensions in simplified models without correlational selection (Lande and Arnold 1983). Third, we refitted the models with only simple effects of behavioural dimensions as no correlational or disruptive selection was detected. This threefold approach allowed us to explore the potential for linear, correlational, disruptive and stabilizing selection without overparametrizing the models. We report results for this last step in the main text (Table 1) and the other steps as supplementary material (Tables S3-S5). The best fitting models were selected using an information-based approach with Akaike's criterion corrected for small sample size (AICc: Burnham and Anderson 2002). The support of each model was the difference in AICc between each model and the model with the lowest AICc (Δ), and AICc weight (w). We then averaged best models (models with $\Delta < 2$) and provide estimates and relative importance for all variables in this set of models. Finally, we estimated both selection gradients

Table 1. Survival status in relation to individual behavioral types (sociability, boldness and exploration-activity), sex and body mass ($n = 217$). Summary of the averaged best models ($\Delta AICc < 2$). For a list of all models with $\Delta AICc$ see Table S1. Variables are all scaled. The estimate for sex is given for males (M).

Parameter	Estimate	p-value	Relative Importance
Intercept	-1.95 [-2.64, -1.25]	< 0.001	–
Sociability	-0.49 [-0.86, -0.12]	0.009	1.00
Sex (M)	0.92 [0.15, 1.68]	0.019	1.00
Exploration- activity	0.10 [-0.30, 0.50]	0.624	0.22
Boldness	-0.06 [-0.42, 0.30]	0.742	0.21

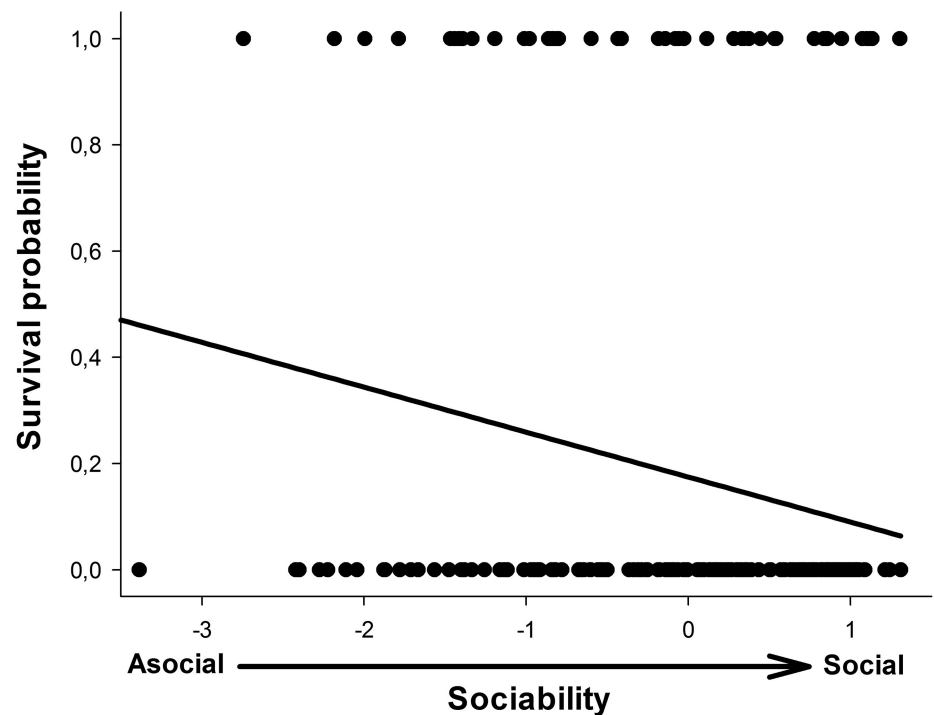


Figure 1. Probability of surviving predators in relation to individual sociability value. Shown are individual survival status and the predicted line as a function of sociability score.

and simple selection differentials (Lande and Arnold 1983). Directional selection gradients were transformed from the logistic regression coefficients to average gradient vectors β_{avggrad} implementing the method described by Janzen and Stern (1998) as the dependent variable was binary. Selection differentials were measured as the average of the trait after selection (thus including only surviving individuals) minus the average of the trait before selection (including both surviving and dead individuals). Selection gradients for quadratic effects were multiplied by two to obtain nonlinear selection coefficients (Stinchcombe et al. 2008).

Results

Mean survival rate was 0.20 ± 0.03 . For the selection analysis, the best models had four predictors: sociability score, sex, exploration-activity and boldness (Table 1, Table S2). However, only the effects of sociability scores and sex were supported by relative importance and estimates statistics. Less social individuals survived more than social ones (Figure 1) and males survived

Table 2. Survival selection gradients and selection differential on sociability and exploration. The averaged best logistic mixed-models retained sociability, exploration-activity, boldness and sex (Table 1) without evidence of correlational selection and weak evidence of stabilizing or disruptive selection (Tables S3, S5). We estimated selection gradients using these predictors (standardized to zero mean and unit variance for sociability and exploration) and experimental group as a random effect. Logistic coefficients were recalculated to average gradient vectors β_{avggrad} according to the methods of Janzen and Stern (1998). Selection differentials S are measured as the average of the standardized trait after selection (thus including only individuals surviving) minus the average of the standardized trait before selection (including both surviving and dead individuals, i.e. 0). The estimate for sex is given for males (M).

Parameter	Estimate \pm SE	Statistics	$\beta_{\text{avggrad}} \pm$ SE	S
Sociability	-0.47 ± 0.18	$z = -2.53, p = 0.011$	-0.06 ± 0.03	-0.41
Exploration -activity	0.10 ± 0.20	$z = 0.50, p = 0.618$	0.01 ± 0.03	0.04
Boldness	-0.06 ± 0.18	$z = -0.34, p = 0.735$	-0.01 ± 0.03	-0.02
Sex (M)	0.96 ± 0.40	$z = 2.42, p = 0.016$	–	–

better than females (males: 0.32 ± 0.06 , females: 0.16 ± 0.03). No interaction terms were retained in the best models (Tables S5) suggesting there was no correlational selection. When analyzing disruptive and stabilizing selection, squared boldness and squared sociability were also retained in the best models (Table S3). However, estimates statistics and relative importance give no support to a quadratic effect of sociability and relatively weak support for a quadratic effect of boldness (Tables S3, S4). Bold and shy fish tended to survive better than fish of intermediate boldness. Overall, while the selection differential was relatively strong for sociability, selection gradients for sociability and squared boldness were relatively weaker (Table 2, Table S4).

Discussion

In this study, we show that asocial mosquitofish survived better than more social mosquitofish in the presence of a predator. One might think that being part of a social group would be the best predator avoidance strategy. Indeed, it is well-known that individuals in shoals benefit from the confusion and dilution effects and thus should have a lower probability of being eaten (Miller 1922; Krakauer 1995). It is also well known, however, that groups of individuals also attract more predators than single individuals (Botham et al. 2005). This might be especially true for naive predators that may have lower abilities to localize novel prey. Shoaling, as a predator avoidance strategy, should thus depend on a benefit-cost balance where confusion-dilution is the benefit and predator attraction is the cost. In our assays, population density was low (8 fish/m^2 – compared to $60\text{--}100 \text{ individuals/m}^2$ in dense populations in the wild, Mills et al. 2004; Goldsworthy and Betolli 2006), so presumably the benefits of safety in numbers were relatively weak (weak dilution/confusion effect) and predators tended to target the groups. If safety in numbers is weak, then asocial individuals might be safer being alone, especially if they are stealthy and thus not attacked, and/or if they are particularly good at escaping attacks. At low density, social individuals, presumably aggregating in small groups, might still attract predators without the strong benefits of shoaling.

The fact that asocial individuals survive better in low conspecific density, combined with our earlier findings that asocial mosquitofish disperse further and have larger ecological impacts than social individuals (Cote et al. 2010a, 2017), is potentially very important for invasion ecology. Since asocials are more likely to disperse and thus being the individuals colonizing new habitat, typically at low density, it is likely that they are responsible for driving the invasion process (Cote et al. 2010a). These results also highlight the importance of sociability in a relatively understudied area of the invasion process, namely survival during dispersal and settlement. During the dispersal and settlement stage of an invasion population densities are supposed to be relatively low. In the context of our results this suggest that asocial individuals would be more suitable invaders since, at low densities, they survive predation better than social individuals. However, with increasing population density the potential for social individuals creating groups large enough to be beneficial for fitness despite increased predator-attraction should also increase. Even though the positive effects of group-living increase, it could still be outweighed by an accelerating predator attack rate on larger groups, or by increased competition in larger groups. We suggest that in low density, as tested here, the benefit/cost ratio of shoaling should be low, explaining why asocial individuals perform better than socials in our study. While we were unable to test for it, we expect the benefit/cost ratio to increase with density which could, in turn, explain why asocials leave populated areas. The possible importance of this mechanism for moving the invasion-front forward is supported by theoretical work (Fogarty et al. 2011) showing that both the speed and severity (counted as invader-density per patch) of an invasion was affected by the mix of personalities in the founding population. To investigate this further, studies should examine BT-dependent survival with predators at a range, from low to high, of prey densities. Another explanation for better survival of asocial individuals could be that individuals with a high likelihood of escaping a predator (e.g. through swimming speed or efficient use of shelter) might be less likely to join social groups as the benefit provided is lower than the costs (i.e. competition and predation attraction), whereas individuals that have poorer escape ability might rely on schooling for increased safety. This has the potential to spatially segregate social and asocial BTs and increase the likelihood of mating within BT, reinforcing behavioural differences between social and asocial individuals. This is especially probable along a biological invasion succession where environmental filtering of phenotypes may generate spatially differentiated phenotypes (Phillips et al. 2006; Brodin et al. 2013).

Survival was also affected by squared boldness, albeit to a much smaller extent, showing that very shy or very bold individuals survived better than individuals exhibiting intermediate boldness. This pattern could, for the very shy individuals, be explained by them staying in refuges and hence

never encountering predators. Very bold individuals, on the other hand, might experience a reduced relative predation risk both through accurate information gathering of the predator's status (mosquitofish engage in predator inspection; Smith and Belk 2001) and through potentially better ability to escape attacks. The latter could either be an effect of enhanced condition due to the competitive foraging advantage of high boldness or because high boldness could be associated with physiological traits suitable for avoiding predation (e.g. quick reactions, fast movement) allowing for high boldness (Michelangeli et al. 2018).

Given that sociability is important for prey survival with predators, a key issue is whether sociability is related to size or sex. Interestingly, we found for these fish (Cote et al. 2011) that the correlation between sociability and body mass was negative for females but positive for males (but see Cote et al. 2010a for no significant relationship between size and sociability). Why should large females and small males be asocial; i.e., tend to avoid joining large groups? For males, smaller individuals might avoid groups because they are at a competitive disadvantage for mating opportunities, while larger males that compete well for mating opportunities might join groups for access to more females. For females on the other hand, large, reproductive individuals might avoid conspecifics to reduce the risk of cannibalism on their future newborns, or to reduce courtship harassment by males. Regardless of why large, potentially gravid, females tend to be asocial, this propensity combined with the tendency for asocial individuals to disperse could be a factor increasing the spread of this invasive species through increased dispersal of live bearing gravid females.

We also found that females were more likely to be eaten by predators than males independent of their body mass and of their BT. This is an intriguing result that might be connected to body-shape dependent escape ability. Males have a more slender body-shape than females, a trait that has been shown to affect important escape traits such as burst speed, maneuverability and ability to hide (Langerhans et al. 2004). In a recent study, McCormick et al. (2018) showed that long-term survival of tropical reef-fish was explained by behavioral trait variation connected to escape ability, where fish that escaped better survived longer. An alternative, or complementary, explanation could be that females, due to heavy courtship by males, are pre-occupied with avoiding male harassment and hence are less perceptive towards predators (Dadda et al. 2005). This finding implies that, at least at the invasion front, females might be the limiting sex when invading environments with high predation pressure. Intriguingly, as mosquitofish females are live bearing, and may store sperm for several months (Constantz 1989), they can invade successfully as a solitary individual. One sperm-storing female might disperse for weeks before settling, and found a new population in a novel patch. However, our results suggest that females might be particularly vulnerable to predation while dispersing,

especially at the low densities often associated with dispersal and initial colonization of new habitats, and hence that predation could be an important factor reducing the frequency of such colonizations.

A general concept in the study of behavioral syndromes is that the performance (fitness or component of fitness) of different BTs should depend on the ecological context. For sociability, an *a priori* hypothesis is that at low density, asocial individuals (that avoid groups) should do better than social individuals, whereas at high density, social individuals should outperform asocial ones (Cote et al. 2010a, b). In the face of predation risk, the more specific hypothesis is that at low density, asocial prey should survive better. Our results corroborate this hypothesis. A future step should be to test the companion prediction that at increasingly higher density, social prey should survive better. These outcomes potentially have important impacts for invasions and other aspects of spatial ecology (e.g., recolonization of ephemeral habitats, metapopulation or metacommunity dynamics; Sih et al. 2012). For invasions, if asocial individuals both disperse more readily (Cote et al. 2010a, 2011), have higher ecological impacts (Cote et al. 2017) and perform better (e.g., survive better with novel predators) at low density in newly colonized habitats, this can be an important mechanism facilitating invasions. In general, more studies on how BT and ecological context interact to determine fitness at “home”, dispersal tendencies, and fitness in newly colonized habitats should prove rewarding.

Ethical standards

All procedures involving handling of fish were permitted by the ethical committee on animal experiments in Davis (Protocol - 06-12142) and comply with current Californian law.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Loadings of behaviours on two principal components.

Table S2. Selection of best models exploring dispersal decision.

Table S3. Survival status in relation to individual behavioural types with linear and quadratic terms.

Table S4. Selection gradients and selection differential with linear and quadratic terms.

Table S5. Survival status in relation to behavioural type and to the interactions between behavioural types.

Table S6. Survival status in relation to raw scores of individual behavioural types.