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Personality-dependent dispersal in the invasive mosquitofish: group composition matters

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Understanding/predicting ecological invasions is an important challenge in modern ecology because of their immense economical and ecological costs. Recent studies have revealed that within-species variation in behaviour (i.e. animal personality) can shed light on the invasion process. The general hypothesis is that individuals' personality type may affect their colonization success, suggesting that some individuals might be better invaders than others. We have recently shown that, in the invasive mosquitofish (*Gambusia affinis*), social personality trait was an important indicator of dispersal distance, with more asocial individuals dispersing further. Here, we tested how mean personality within a population, in addition to individual personality type, affect dispersal and settlement decisions in the mosquitofish. We found that individual dispersal tendencies were influenced by the population's mean boldness and sociability score. For example, individuals from populations with more asocial individuals or with more bold individuals are more likely to disperse regardless of their own personality type. We suggest that identifying behavioural traits facilitating invasions, even at the group level, can thus have direct applications in pest management.

Keywords: behavioural type; social tendency; ecological invasion; dispersal; behavioural mix

1. INTRODUCTION

Ecological invasions are gaining attention as a major threat to biodiversity and an important element of global change [1]. Ecological invasions occur when species introduced to areas beyond their native range spread from the point of introduction and become abundant. At high densities, invasive species often have substantial negative impacts on native species [2,3]. Identifying conditions that facilitate invasions therefore represents a crucial research area [4].

A potentially innovative approach for understanding invasions combines behavioural ecology and invasion ecology by focusing on how individual variation in personality traits within species [5,6] might influence invasion dynamics [7–10]. In particular, several studies have documented personality-dependent dispersal, where dispersers tend to be, for example, bolder (e.g. [11]), more aggressive [7] or less sociable [10,12] than individuals that remain behind. For invasions, this has the potentially important implication that invaders colonizing a new site (at the leading edge of an invasion or range expansion) will tend to be more aggressive or asocial than average. Depending on conditions in the new site, this could substantially affect the invaders' establishment success or subsequent ecological impacts on the invaded community [7,13].

When dispersal depends on the focal individual's sociability, this suggests that both dispersal from one site and settlement in a new site depend on social interactions in both sites. Although an earlier study showed that social interactions and their effect on dispersal depend on individual variation in social behaviour [10], it did not examine how effects of social interactions on dispersal might also depend on the personalities of other individuals in the population. An exciting hypothesis, for example, is that dispersal might depend on variation in affiliative behaviour or group cohesion (e.g. shoaling) in both sites [14] or on expected fitness outcomes that could depend on the mix of personality types in the population [15]. Even more intriguingly, dispersal might depend on an interaction between the average personality of the social group (e.g. its aggressiveness or sociability) and the personality of the potential disperser.

Individual variation in sociability also potentially adds a density-dependent element to personality-dependent dispersal and settlement. Asocial individuals should avoid (i.e. disperse away from) high-density sites, and settle preferentially in lower-density sites [12]. Conversely, social individuals should be less likely to disperse from high-density sites, but should settle preferentially in high-density sites. This predicted pattern can then have important implications for the dynamics of a multi-stage invasion (introduction, spread, establishment, growth to high density, and high impact on an invaded community [16]) where different behavioural characteristics probably affect a species's success at each stage of the invasion process. For example, asocial or aggressive individuals may have greater success establishing in newly colonized habitats, while social or unaggressive ones may cause a population to grow rapidly to high density, where its impacts on the native community may be the most severe [7,10]. The key prediction, however, that density and personality interact in governing both dispersal and settlement has rarely been tested [12].

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We recently found that individual mosquitofish (*Gambusia affinis*) tend to display consistent sociability, boldness, activity and exploration behaviours over time (i.e. personalities), and significant positive correlations between all personality traits [10]. Most notably, sociability was an important indicator of dispersal distance, with more asocial individuals dispersing further [10]. Here, we test how mean personality within a population changes personality-dependent dispersal in the mosquitofish. Our focal individuals were randomly divided into eight populations, creating variation in the average personality between groups. We measured sociability (tendency to shoal), boldness (latency to emerge from refuge), exploration tendency and activity (movement in a novel environment), and dispersal decisions in experimental streams in all individuals. This design allowed us to test the effect of mean population personality scores on dispersal decisions of individuals as a function of individual personality type. Our design also included two density treatments to explore interactions between population density and population composition on dispersal decisions. Finally, based on our previous results, we assumed that some individuals prefer to colonize empty habitat while others would prefer to join an already existing population. We therefore created a situation in which dispersers could join an established population after their first dispersal event or could continue moving to colonize empty habitats. We tested for individual consistency in behaviour by repeating behavioural assays four to five months later. To summarize, we predict (i) that mean population personality scores and population density will modulate the effect of individual personality type on dispersal decisions, and (ii) that individual personality type affects the probability of joining a novel population after the departure from the initial population.

2. MATERIAL AND METHODS

Four hundred and seventy-two mosquitofish (approx. 1/3 males and 2/3 females) 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 15 August 2008. They were held in groups of 60 in 80 l flow-through fibreglass tanks on a natural photoperiod (for early May, L/D = 14/10) at 22°C and fed Tetramin flakes *ad libitum*. Mosquitofish were acclimated to these conditions for more than three weeks prior to behavioural observations, which were carried out between 3 and 10 September 2008 and between 15 and 25 October 2008.

Two weeks prior to behavioural observations, individual mosquitofish were marked with elastomer tags (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 four locations on the caudal peduncle (two on each side). Fish were allowed to recover from anaesthesia in an opaque bucket before being transferred back to their home aquaria. No differences in mortality rate were observed between marked and unmarked fish (marked fish: 2.5% over 2 days; unmarked fish: 2.7–6.3% over the same 2 days), and we checked for normal behaviour after marking by confirming that behaviour was similar between sets of unmarked and marked fish (see [10]).

One night before behavioural observations began individual mosquitofish were placed 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. Twenty females and 10 males were run through personality characterizations each day. We ran 472 individuals over four periods of 4 days (on the last day of each period we only ran 28 fish). This sex ratio matched the sex ratio in the fish collected randomly from the vector control district. We ran two behavioural assays to characterize behavioural types (BT) and then their dispersal tendency was measured in artificial streams (see detailed methods below).

(a) *Tendency to shoal (sociability)*
Here, we recorded the amount of time spent near a shoal of conspecifics [10,17]. 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. We used six predetermined stimulus shoals comprising 14 mosquitofishes (seven females and seven males). Because the composition of a stimulus shoal could influence sociability scores of focal individuals, each population for dispersal assays (see below) contained the same number of focal fish tested with each of the six stimulus shoals. One of six predetermined stimulus shoals was introduced into one of the smaller compartments 1 h before the experiments began, while the other small compartment was left empty as a control. After 1 h, the focal fish was introduced into the centre of the larger compartment and allowed to acclimate for 10 min. Black curtains with a small slit surrounded the aquarium and allowed us to observe fish without disturbing them. The position of the focal fish was continuously recorded for 10 min using 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 [17]. When the assay was complete, individuals were returned to their individual home aquarium.

(b) *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 [18,19]: 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-flowerpots 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 on the opposite end from the flowerpots. 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 s).

Boldness was the log(2700 s; the maximum time allowed for fish to exit the refuge) minus log(latency (s) to exit from refuge, and to stay for more than 10 consecutive seconds out of refuge); shorter latency to exit indicates higher boldness. Exploratory tendency was quantified by area covered

(see below), and activity was measured as percentage of time spent moving during the 5 min after the fish exited the refuge.

While some have suggested that latency to emerge in a novel environment should be termed exploratory behaviour and not boldness [20], we follow several earlier papers (e.g. [18,19]) in our assessment. 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 well measured by space use after emergence from refuge. While we would like independent assessments of exploration and activity, in fact the two might not be functionally separable. To explore, animals must be active. To differentiate 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 an appropriate measure of space use.

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 5 min assay. The percentage of time that the fish spent moving was the percentage of frames in which the fish moved more than 1 body length from its position in the previous frame. 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.

(c) Body mass measurement and density treatments

At the end of each observation day, mosquitofish were weighed to the nearest 0.001 g. Unfortunately, we could not measure body length in this experiment. After 30 fish were observed, they were transferred to two 80 l fibreglass tanks with approximately 73 per cent of the fish going into one tank and approximately 27 per cent in the other. Each day, eight fish were transferred from their individual tanks to the low-density treatment tank (except the last day where only six fish were released) and 22 fish were transferred to the high-density treatment tank. The sex ratio was kept similar in the two tanks over the 4 days of behavioural observations. After the 4 days of behavioural assays, one tank contained 30 fish and one contained 88 fish. Fish were randomly distributed among the two density treatments, but behavioural types did not differ between high- and low-density treatments ($p > 0.05$ for all). Five days after the end of the behavioural assays, these two groups were placed in two different experimental streams for the dispersal assay.

(d) Dispersal assay

The dispersal assay was conducted in two artificial streams at CABA using the same basic methods as in our earlier study [10]. Each stream consisted of five plastic pools (each 1.5 m diameter, filled with 40 cm of well water) connected by riffles (1.3 m long, 30 cm wide). The streams were located outdoors under a roof with open sides (about 5 m high) that screened out rain and direct sunlight. A 34 HP pump at the downstream end pumped water ($370.7 \, \text{ml s}^{-1}$) to the top pool where it then flowed downstream through the system. Pools simulated slow-moving backwaters typically inhabited by *Gambusia*, whereas flow in the riffles was too fast for mosquitofish to maintain position or to swim upstream against. Each pool had three half-flowerpots and three PVC pipes that served as refuges. Water temperature was checked immediately before fish introduction; because we provided a continual input of well-water, water temperature was consistent between streams and among trials (19°C).

Each population of fish was introduced into the most upstream pool, where a removable barrier at the downstream end kept the fish from dispersing while still permitting water to flow out into the riffle. Fish were allowed 2 h acclimation in the pool, after which the barrier was removed and fish were free to disperse or stay in the pool. The flow of water downstream precluded movement upstream, so fish that dispersed out of an upstream pool were unable to return. To examine the difference between joining and invading behaviours (i.e. joining an already existing population versus colonizing an empty habitat), we also added a population in the second pool. This population was composed of 60 randomly chosen fish (20 males and 40 females). We chose this intermediate density based on the hypothesis that individuals leaving high-density populations might search for low-density populations, while individuals leaving low-density populations might search for high-density populations [12]. Although it would have been useful to create two density treatments in the second pool with a full factorial design, the number of populations (and fish) required was prohibitively high. For the same reason, we were unable to assess the BTs of these non-focal fish. We could not prevent the dispersal of non-focal fish from the second pool (referred to hereafter as 'non-focal population') without interrupting the dispersal of focal fish. We dealt with this potential problem by introducing, one day before the dispersal assay of focal fish, the non-focal populations in the second pools of each stream, and we allowed these fish to disperse for 24 h. Then, we captured dispersers from each non-focal population and released them in the non-focal pool (pool 2) of the other stream to retain an intermediate density (around 60 fish), as the number of dispersers from the two non-focal populations was similar. We chose 24 h based on previous experiments where the number of dispersers stabilized after a 24 h period. We then released the two groups of focal individuals as previously described. After 24 h, we collected the fish and recorded the pool in which each individual was captured. The two groups were then kept in outdoor tanks (in groups of seven) and were used in a predation experiment (T. Brodin, J. Cote, S. Fogarty & A. Sih 2009, unpublished data).

Four blocks of 118 individuals (one population of 30 individuals and one of 88) were run through behavioural and dispersal assays over 4 days. After four to five months, the survivors (46 individuals survived in the outdoor tanks and then in the predation experiment) were then run again through the personality assays to test for individual consistency (4 days between 4 and 9 February).

(e) Statistics

Sociability score for three individuals and boldness score for two individuals are missing because of problems in the recording process. We thus excluded these individuals from the analysis. Also, six individuals (for which two boldness scores were missing) never emerged from shelter during the novel environment assay and therefore could not be assessed for exploration/activity. They were thus excluded from the

PCA (see below) and dispersal analyses. Including these six animals in an analysis that directly used behavioural metrics instead of PCA axes did not alter the qualitative conclusions on effects of sociability and boldness on dispersal. A total of 463 fish remained for analyses.

(f) Behavioural correlations and consistencies

To test for correlations between personality parameters, we calculated pairwise correlations among the four personality parameters (sociability, boldness, exploratory behaviour and activity). Consistency in the four behaviours measured across a four-month time period was tested with Spearman's rank correlations.

(g) Principal component analysis

Because our behavioural metrics were correlated (see §3), we performed a principal component analysis (PCA) with varimax rotation [21] in JMP v. 7 to define possible personality trait dimensions. Based on the scree plot, we identified three key PCA factors for further analyses [22]. Behaviours with a loading of at least 0.32 were considered to contribute to a component [23]. The relationships between principal components and sex and body mass were analysed using a general linear model (Proc GLM) with body mass and sex as explicative variables.

(h) Dispersal decisions

Because there was a non-focal population in the second pool, we analysed dispersal decisions in two steps. First, we analysed factors influencing the probability of leaving the initial population (pool 1) using a binomial variable ('dispersers' = individuals leaving pool 1; 'residents' = individuals staying in pool 1). Second, we analysed factors affecting the probability of dispersers leaving pool 2 using a binomial variable ('joiners' = individuals staying in pool 2; 'invaders' = individuals leaving pool 2). This second analysis examined settlement decisions following a dispersal decision. We analysed the relationship between dispersal decisions and 'individual PCA scores' and 'population PCA scores'. Population PCA scores, or population personality scores, were calculated for each individual as the mean personality scores within the population excluding the score of the focal individual. Therefore, population personality scores are independent of individual personality scores ($p > 0.20$ for all PCAs), and the effects of population personality scores and of individual personality scores on individual dispersal decisions are not confounded. We performed these analyses of individual dispersal decisions using a mixed generalized linear model with a logit-link and a binomial error distribution in SAS [21,24]. The fixed effects were individual PCA scores, population PCA scores, density treatment, body mass, sex and the interactions. In particular, we added the interactions between individual PCA scores and population PCA scores, and the interactions between density treatment and PCA scores (individual and population). We also included a random effect for the experimental population nested within the density treatments. This random effect controls for differences between populations and for common causal factors that may influence independent dispersal decisions of individuals from the same population [24,25]. We also added a random effect controlling for the period of the year when these assays were conducted (between 3 and 10 September 2008 versus between 15 and 25 October 2008). We used type III F tests for fixed effects.

Table 1. Consistency (Spearman's rank correlation) of the four behaviours measured across a four-month time period ($n = 46$).

	rank consistency
sociability	0.30, $p = 0.05$
boldness	0.41, $p = 0.007$
exploratory behaviour	0.29, $p = 0.06$
activity	0.45, $p = 0.003$

Table 2. Correlations between the four behaviours measured before the dispersal assay ($n = 463$). Correlation coefficients are given.

	boldness	exploratory behaviour	activity
sociability	0.18, $p < 0.001$	0.15, $p = 0.001$	0.07, $p = 0.15$
boldness		0.25, $p < 0.001$	0.21, $p < 0.001$
exploratory behaviour			0.79, $p < 0.001$

The model was simplified by using backward elimination of the non-significant terms.

These individual-based analyses allow us to estimate the effect of the personality of others independently of the effect of individual personality scores on individual dispersal decisions. Mixed models, with populations as a random effect, are commonly used when information at the individual and population levels are needed, and to control for the lack of 'independence' between individuals of the same population. We also ran simple analyses on population mean dispersal rate to predict how the number of dispersers can be influenced by the composition in personality at the population level. We analysed how mean dispersal rate (number of dispersers divided by total number of individuals in the population) and mean joining rate (number of joiners divided by total number of dispersers) depended on mean personality scores in the population (general linear model). Since the sample size is now only eight populations (instead of 463 individuals), these analyses are more conservative but less powerful.

3. RESULTS

Fish exhibited a behavioural consistency over time and across contexts. Individuals displayed significant rank order consistency over four months in all four behaviours assayed (table 1). However, individuals displayed nearly significant repeatability in exploratory behaviour: ($p = 0.06$). The four behaviours were significantly positively correlated to each other with the exception of a non-significant correlation between sociability and activity (table 2). A scree plot of the PCA revealed three factors that explained 95.2 per cent of the variance (table 3). We retained all three factors because the third factor explained as much variance as the second and was the only factor representing individual variation in boldness. PC1 had strong component loadings for exploration and activity, PC2 represented sociability, while PC3 represented boldness (table 3). Fish that had higher PC1

Table 3. Component loadings of behaviours observed on two orthogonally rotated principal components. Boldface indicates the highest component loadings for each behaviour.

behaviour	principal components		
	exploration and activity	sociability	boldness
sociability	0.08	**0.99**	0.08
boldness	0.14	0.08	**0.99**
exploratory behaviour	**0.93**	0.12	0.14
activity	**0.95**	0.02	0.10
% variance explained	44.8	25.2	25.2
% total variance	95.2		

scores explored a larger area and spent more time moving. Fish that had higher scores on PC2 spent more time close to the shoal and fish that had higher scores on PC3 took less time to emerge from the shelter. We analysed the dependency of personality scores on body mass and sex. Boldness scores were lower and exploration and activity scores were higher in females than in males (boldness: $F_{1,461} = 4.15$, $p = 0.04$; exploration and activity: $F_{1,461} = 5.15$, $p = 0.02$), but these scores were not correlated to body mass (boldness: $F_{1,460} = 0.33$, $p = 0.57$; exploration and activity: $F_{1,460} = 1.20$, $p = 0.27$). Sociability scores depended on the interaction between body mass and sex (body mass: $F_{1,459} = 5.64$, $p = 0.018$; sex: $F_{1,459} = 0.0001$, $p = 0.99$; body mass x sex: $F_{1,459} = 24.09$, $p < 0.0001$). The relationship between sociability scores and body mass was positive in males (estimate: 5.26 ± 1.52, $F_{1,156} = 11.95$, $p = 0.0007$) and negative in females (estimate: -1.83 ± 0.37, $F_{1,303} = 24.93$, $p < 0.0001$). Body mass and sex were included together as explicative variables in the previous models. However, because of the relationship between sex and body mass, the effect of these variables may not be distinguished. For boldness and exploration and activity, we also ran separated analyses on the relationship between body mass and personality scores for females and males. Boldness and exploration and activity scores were not related to body mass in females nor in males ($p > 0.32$ for all the effects).

Corroborating our previous work [10] we again found that dispersal decisions were related to individual sociability score (table 4). Asocial individuals dispersed more from the first pool (figure 1). Interestingly, individual dispersal decision also depended on the mean personality scores within the population (excluding the focal individual) regardless of the personality of the focal individual. Individuals dispersed more frequently from populations where individuals were more asocial and bolder on average (figures 2 and 3). The effects of mean personality scores within the population were independent of the individual personality scores ($p > 0.5$ for all the interactions between mean population personality scores and individual personality scores). Dispersal decision was not related to body mass or sex (table 4). Density did not affect overall dispersal probability or personality-dependent dispersal (table 4; $p > 0.39$ for all interactions between density and individual or population personality

Table 4. Individual dispersal decision (leaving pool 1) depending on population density, individual personality traits and mean personality scores in the population. Random effects: population (density) and block (September versus October). Estimates are given for high population density (HD) and for female (F).

	estimates ± s.e.	F statistics
intercept	-0.34 ± 0.10	—
density (HD)	-0.14 ± 0.30	$F_{1,6} = 0.23$, $p = 0.6468$
individual exploration and activity	-0.03 ± 0.11	$F_{1,446} = 0.10$, $p = 0.757$
individual sociability	-0.22 ± 0.10	$F_{1,451} = 5.07$, $p = 0.025$
individual boldness	-0.02 ± 0.10	$F_{1,447} = 0.04$, $p = 0.846$
mean pop. exploration and activity score	0.56 ± 0.90	$F_{1,448} = 0.39$, $p = 0.535$
mean pop. sociability score	-1.84 ± 0.93	$F_{1,451} = 3.96$, $p = 0.047$
mean pop. boldness score	2.28 ± 0.85	$F_{1,451} = 7.18$, $p = 0.008$
sex (F)	-0.27 ± 0.21	$F_{1,450} = 1.70$, $p = 0.193$
body mass	1.39 ± 0.86	$F_{1,449} = 2.63$, $p = 0.105$

scores). The analysis using mean dispersal rate confirmed the patterns observed about mean population personality traits. Dispersal rate depended on mean sociability score (estimates: -0.60 ± 0.24, $F_{1,4} = 5.80$, $p = 0.07$) and mean boldness score (estimates: 0.49 ± 0.15, $F_{1,4} = 10.84$, $p = 0.03$) but not on mean exploration and activity score (estimates: 0.18 ± 0.17, $F_{1,4} = 1.14$, $p = 0.35$). Although the effect of population mean sociability on dispersal was only borderline significant, it is worth noting that mean sociability score and mean boldness score explained 31 and 62 per cent, respectively, of the variance in dispersal rate for these eight populations.

After arriving in pool 2, dispersers could stay in this new population of intermediate density or choose to continue dispersing. This decision depended on the mean exploration and activity score in their initial population. Dispersers kept moving when they had left a population where individuals were more active and exploratory on average (table 5). This decision did not depend on any other personality score (individual or population). Dispersers from high-density pools left the new population more often than dispersers from low-density pools (table 5). Finally, females and individuals of lower body mass left the new population more often (table 5). The analysis using population means was unable to detect an effect of mean population personality on mean dispersal rate from the second population (effect of mean sociability score: $F_{1,4} = 0.002$, $p = 0.97$; boldness score: $F_{1,4} = 1.13$, $p = 0.39$; exploration and activity score: $F_{1,4} = 0.39$, $p = 0.57$); however, with only four degrees of freedom, these tests had low statistical power.

4. DISCUSSION
(a) *Individual personality scores*
Consistent with our previous study [10], mosquitofish exhibited two key components of personality traits.
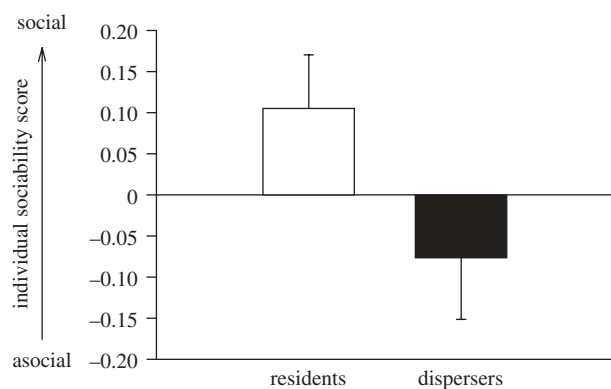
Figure 1. Mean individual sociability value in relation to dispersal status. Shown are mean values ($\pm$s.e.) of the sociability score as a function of the dispersal status (residents, individuals that stayed in pool 1; dispersers, individuals that left pool 1).
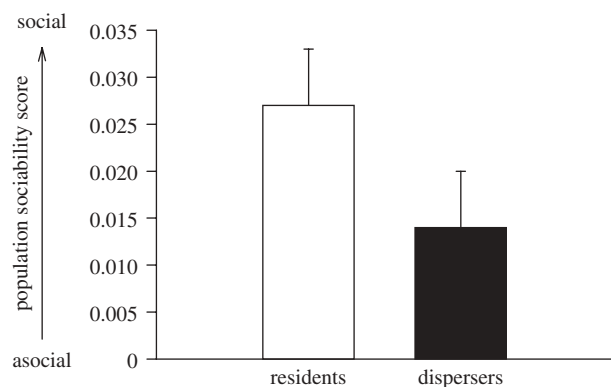

Figure 2. Mean sociability value in the initial population in relation to dispersal status. Shown are mean values ($\pm$s.e.) of the population sociability score as a function of the dispersal status (residents, individuals that stayed in pool 1; dispersers, individuals that left pool 1).

With regard to behavioural consistency, rank order correlations were significantly positive (or nearly so; exploratory behaviour: $p = 0.06$) for all four behavioural metrics over four months; individual differences in behaviours were therefore consistent even if these rank order correlations were less strong than the ones found after three weeks [10]. Behavioural types might be less consistent across major transitions in the life of an animal (however, see [26]) but are still fairly consistent for long periods of time. Fish have also been kept in outdoor tanks and were used in a predation experiment. These events can also explain the lower consistency. We also found that mosquitofish generally display positive correlations between measures of sociability, boldness, exploration and activity. It is worth noting that boldness, exploration and activity were measured in the same assay, suggesting that the non-independency of these measures could explain the observed behavioural correlations (in particular, for activity and exploration). However, boldness and exploratory behaviour were positively correlated to sociability while there was no correlation between activity and sociability. This result reinforced the idea that sociability is a behavioural trait that is partly independent of other behaviours.
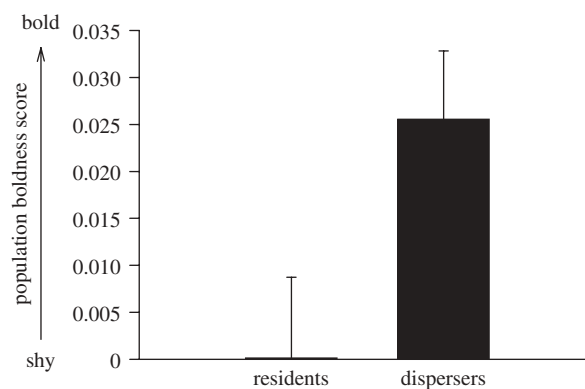
Figure 3. Mean boldness value in the initial population in relation to dispersal status. Shown are mean values ($\pm$s.e.) of the boldness score as a function of the dispersal status (residents, individuals that stayed in pool 1; dispersers, individuals that left pool 1).

Contrary to our previous study, personality traits were correlated with body mass and/or sex. Previous studies in another poeciilid species showed that smaller fish are bolder than larger ones [27] and males are bolder than females [19]. Small fish are often more vulnerable to predation and should thus be shyer. On the other hand, while metabolic rates are positively correlated to body mass in many species [28–30], metabolic rate per gram of body mass decreases with increasing body size [27,31]. Therefore, smaller/younger fish have a faster metabolic rate and are constrained to be bolder to acquire additional resources. In our study, only sociability was related to body mass. Heavier males were more social than lighter males, while the opposite relationship was observed for females. As age is correlated to body size (body mass in our study), heavier/older males may benefit from being more social as it provides greater access to females, while heavier/older females may avoid conspecifics to reduce cannibalism of their future offspring [32]. It is worth noting that body mass may also depend on reproductive status in females. Unfortunately, we have no measurement of body size in this experiment. However, gravid females should also avoid conspecifics to reduce cannibalism. Alternatively, size-assortative shoaling [33], which can enhance the anti-predator benefits of shoaling, may drive sociability differences. Mid-sized individuals may be more common, and thus more likely to shoal, leaving undersized males and oversized females without enough proper shoaling partners. Finally, females and males may be different in the body-mass-dependent benefits/costs of shoaling (e.g. foraging and anti-predator abilities). In addition, females were shyer and more exploratory-active. This result could be explained by the fact that, in an unpublished study, we found that females were more likely to be eaten by predators than males independent of their body mass (T. Brodin, J. Cote, S. Fogarty & A. Sih 2009, unpublished data). There are many potential explanations for these results, but additional work will be necessary before we can discriminate between these competing hypotheses.

(b) *Departure and settlement decisions*

It is notable that here, as in a previous study on mosquitofish [10], sociability was again related to dispersal

Table 5. Individual decision to continue dispersing after arriving in a new population (pool 2) depending on population density, individual personality traits and mean personality scores in the population. Random effects: population (density) and block (September versus October). Estimates are given for high population density (HD) and for female (F).

	estimates ± s.e	F statistics
intercept	−0.37 ± 0.47	—
density (HD)	1.12 ± 0.43	$F_{1,7} = 6.38$, $p = 0.035$
individual exploration and activity	0.18 ± 0.16	$F_{1,179} = 4.48$, $p = 0.276$
individual sociability	0.04 ± 0.15	$F_{1,177} = 0.07$, $p = 0.792$
individual boldness	0.08 ± 0.16	$F_{1,178} = 0.26$, $p = 0.608$
mean pop. exploration and activity score	3.41 ± 1.50	$F_{1,180} = 5.17$, $p = 0.024$
mean pop. sociability score	0.35 ± 2.18	$F_{1,175} = 0.02$, $p = 0.882$
mean pop. boldness score	−0.35 ± 1.68	$F_{1,176} = 0.04$, $p = 0.835$
sex (F)	0.86 ± 0.37	$F_{1,180} = 5.31$, $p = 0.022$
body mass	−2.72 ± 1.33	$F_{1,180} = 4.20$, $p = 0.042$

decisions. Asocial individuals dispersed more than social ones from their population of introduction. A similar pattern has been documented in lizards and humans [9,12,34]. More broadly, our new results further corroborate the general notion that individual dispersal tendency might be related to individual personality (e.g. sociability, aggressiveness or boldness [9]).

In addition, we found that individual dispersal tendencies were influenced by the population's mean personality score (excluding the focal individual score). Individuals living in populations with more asocial individuals or with more bold individuals were more likely to leave, irrespective of their personality scores. To emphasize, this result is not simply saying that since asocial individuals tend to disperse more, populations with more asocial individuals tend to have more dispersers. Social individuals were also more likely to leave if they were in a population with low mean sociability or high mean boldness. Indeed, dispersal decisions are analysed at the individual level and the population's mean personality scores exclude the personality score of the focal individual. In other words, we analysed whether an individual decides to disperse or not depending on population's mean personality scores, the latter scores being completely independent of the scores of the focal individual (see §2 for further explanation). Population's mean sociability scores therefore influence individual dispersal decision independently of the numerical consequences of asocial individuals being more likely to disperse. We also ran a population-based model with the eight populations as statistical individuals. In these analyses, the effect of individual personality scores and mean population scores are confounded. However, there was no effect of individual boldness score in this study nor in a previous one [10], but we found a strong effect of mean personality score in the population. By using both analyses, we can conclude that population composition in personality traits affects dispersal decisions. Moreover, these results might have general implications as they show that using the two mean personality scores in a population allows prediction of dispersal rate in this population.

At least two mechanisms could explain why dispersal decisions depended on boldness and sociability population scores. These two mechanisms are based on the idea that the benefits of sociability vary with social context (i.e. mean population personality scores, others' dispersal decisions). First, asocial individuals are less likely to join shoals and bolder individuals might be more active and out of shelter. Populations with lower mean sociability or populations with higher mean boldness should thus have shoals that are smaller and perhaps less tight. In such a situation, social individuals might have reduced benefits of being in a school (i.e. food localization and confusion/dilution effects for predators [35,36]) and might thus disperse more than if they were in populations with higher mean sociability or populations with lower mean boldness. Second, because asocial individuals displayed a higher dispersal probability, more individuals (the asocial ones) leave from populations where the mean sociability score is lower. Social individuals from those populations might decide to follow this dispersal flow because of its possible information content (i.e. it may suggest that the current patch is of low quality [37]), or because of the protective role of dispersing in groups (i.e. same benefits than the ones of living in groups), or more generally because of 'social facilitation/influence' [38].

Interestingly, mean population personality scores were also significantly (or nearly significantly) related to dispersal rate when we ran analyses at the population level with a sample size of eight populations. In particular, mean sociability and mean boldness scores explain more than 90 per cent of the variance in dispersal rate. While this general linear model cannot determine whether individual personality traits or population composition explained dispersal rate, the combined results of our individual and population-based analyses show that dispersal decisions depend on both individual sociability score and population composition in boldness and sociability.

Based on previous studies we also predicted that some dispersers would prefer to colonize empty habitat while others would prefer to join an already existing population. We therefore created a situation in which dispersers could join an established population after their first dispersal event or could continue moving to colonize empty habitats. We predicted that social dispersers would be more likely to settle in the new population than asocial dispersers, but our results did not match this prediction. Variation in tendency to stay in the new population (in the second pool) might be heavily influenced by the social composition of the new population; however, logistical constraints on the number of mosquitofish that could be run through behavioural assays in a reasonable amount of time precluded us from obtaining these data. Interestingly, however, our individual-based analyses suggested that dispersers from populations with a higher mean exploration and activity score settle less in the new, non-focal populations. More detailed observations

on behaviours associated with dispersal will be needed to explain this pattern.

We also manipulated population density in the initial populations. However, we found no significant effect of population density on dispersal decision and no significant interaction between personality scores and density on dispersal. This is in contrast to studies in other systems often showing density-dependent dispersal (reviewed in [39,40] and another study showing that asocial individuals disperse more from high-density populations while social individuals disperse more from low-density populations [12]. Our inability to detect either density or density × personality effects might be owing to our high- and low-density treatments being too similar, as confirmed in another unpublished study (J. Cote, S. Fogarty, T. Brodin & A. Sih 2009, unpublished data).

We also created a population of intermediate density in the second pool, to satisfy the habitat preferences of dispersers from low- and high-density populations which might prefer higher and lower densities, respectively. Individuals from either a high or low initial population density should thus be equally likely to stay in this second pool of intermediate density. In fact, individuals coming from a low-density population settled more often in the non-focal population than did individuals from a high-density population. This result may be explained by the possibility that mosquitofish dispersing from high-density populations may not have perceived this intermediate density as being significantly different from the population they left initially (100% increase in population density for fishes moving from low density ($n = 30$) to intermediate density ($n = 60$) but 32 per cent decrease in population density for fishes moving from high density ($n = 88$) to intermediate density).

Finally, we found that females and smaller dispersers settled less than males and larger dispersers in the non-focal populations. As body mass/body size is a common predictor of competitive ability, smaller individuals may be attempting to avoid competition and would thus join a new population less often. Females, on the other hand, may also be hesitant to join a new population if they are currently storing sperm or are gravid, as cannibalism of young is frequently observed in this species [32]. This suggests that, independent of their personality traits, females and smaller individuals are more likely to invade new habitats that initially have few conspecifics.

(c) Consequences for biological invasions

We previously suggested that invasions that rapidly spread to pest proportions occur most readily when a species includes a mix of asocial and social dispersers via a process analogous to ecological succession [10,13]. Our hypothesis is that asocial individuals are the first to colonize and subsequently settle in empty patches. Their tendency to stay in low-density conditions allows the population size to increase, facilitating the settlement of social individuals (i.e. joiners). These social joiners increase local density, driving out asocial individuals who disperse and colonize additional empty patches. Until now, our empirical data only confirmed that asocial individuals are the first to colonize empty habitats. Here, we show that personality-dependent dispersal is not a strict individual-centred process. Social individuals also

disperse more when they are surrounded by more asocial/bold individuals, perhaps because of their tendency to use socially acquired information. Asocial individuals, on the other hand, should still be faster or more numerous dispersers as they may be more focused on private information. Our results thus provide support for our previously proposed invasion model.

Identifying conditions that facilitate invasions can also have direct applications, in particular in species that are still being widely introduced. Mosquitofish are listed as one of the world's 100 worst invasive species [41]. When releasing mosquitofish as biocontrol agents, it might be useful to identify factors driving the species spread past its intended target area. We previously suggested that individual personality score might help to predict dispersal propensity [10]. However, logistical constraints would probably preclude vector control agencies from obtaining individual personality scores. Here, we show that the mean population personality scores of released groups could be used to predict dispersal rate after introduction. The assessment of such group behavioural types might be possible through quick observations of the released groups (i.e. tightness of the group, number of individuals out of the shelter, dispersal rate in an artificial stream). We acknowledge the fact that our studies are made in artificial streams and that further studies are needed to validate our results in natural conditions. However, our results highlight the role of behavioural traits, at the individual and at the group level, in the spread of an invasive species.

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