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Personality-dependent dispersal cancelled under predation risk

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Dispersal is a fundamental life-history trait for many ecological processes. Recent studies suggest that dispersers, in comparison to residents, display various phenotypic specializations increasing their dispersal inclination or success. Among them, dispersers are believed to be consistently more bold, exploratory, asocial or aggressive than residents. These links between behavioural types and dispersal should vary with the cause of dispersal. However, with the exception of one study, personality-dependent dispersal has not been studied in contrasting environments. Here, we used mosquitofish (*Gambusia affinis*) to test whether personality-dependent dispersal varies with predation risk, a factor that should induce boldness or sociability-dependent dispersal. Corroborating previous studies, we found that dispersing mosquitofish are less social than non-dispersing fish when there was no predation risk. However, personality-dependent dispersal is negated under predation risk, dispersers having similar personality types to residents. Our results suggest that adaptive dispersal decisions could commonly depend on interactions between phenotypes and ecological contexts.

1. Introduction

Dispersal is a fundamental life-history trait that affects ecological invasions, gene flow, species' distributions and species' ability to track favourable environmental conditions [1–3]. A common idea is that, for a given environmental context, a species exhibits a more or less fixed dispersal tendency. In recent years, however, studies have begun to recognize that variation among individuals can be as important for dispersal as the species's average behaviour [1–3]. This idea suggests that dispersing individuals are not a random subset of the population; instead, dispersers might often differ from non-dispersers in having morphological, physiological or behavioural specializations that increase dispersal success [1–3]. This view is summarized in the notion of dispersal syndromes, which can be defined as the covariation of several phenotypic and life-history traits associated with dispersal decisions [4]. Among these traits, the importance of personality traits in dispersal decisions/success has recently been emphasized [5–9].

Personality traits are between-individual differences in behaviours consistent across time and contexts [10,11]. These differences are related to various life-history traits and can therefore be important in both population and ecological processes [12–14]. For example, personality traits can influence the dispersal process through modifications of departure propensity, transience capacity or facilitation of settlement [5]. This results in emigrants, immigrants or colonizers being more bold, exploratory, asocial or aggressive than residents or locally born individuals [7–9,15,16] (reviewed by Cote *et al.* [5]).

It is known that multiple causes such as mate competition, resource competition and predation risk can influence an individual's propensity to disperse from or settle in a given site [17]. As personality types differ in their abilities

to cope with these ecological factors, the relationship between personality traits and dispersal behaviour should therefore depend on the ecological and social factors motivating dispersal. For example, in common lizards (*Zooteca vivipara*), asocial individuals, who have increased fitness at low density, disperse when densities get too high, while social individuals, who have increased fitness at high density, disperse when densities are too low [6,18]. Although the hypothesis that the relationship between personality traits and dispersal behaviour depends on factors driving dispersal has only been tested once, it is likely to be a more general phenomenon.

Here, we used western mosquitofish (*Gambusia affinis*) to test whether personality-dependent dispersal varies with predation risk. After measuring several personality traits (sociability, exploration/activity and boldness), we created groups of mosquitofish and tested individual propensities to disperse in artificial streams where variation in predation risk is represented by the presence or absence of a caged trout in the mosquitofishes' initial pools.

Numerous theoretical and empirical studies have shown that increased predation risk induces higher dispersal rates [19–22]. However, dispersing can be more costly or less beneficial than staying if, for example, predators are widely distributed, predation risk is high or crossing initial habitat to disperse exposes animals to particularly high risk [22–24]. Ecological contexts can thus explain shifts from predator-induced to predator-suppressed dispersal. These two dispersal reactions to predation risk can also coexist within a species if individuals differ in antipredator defences, individual ability to escape predators or individual likelihood to be targeted by predators. Because an individual's personality influences its vulnerability to predation risk [25–27], personality-dependent dispersal is likely to be mediated by predation risk.

Several hypotheses exist on the expected effect of predation risk on personality-dependent dispersal. First, the relationship between boldness and dispersal from pools with predators could go either way. If shy individuals are more predation-risk-averse or have lower abilities to escape predators, they might disperse to avoid predators. However, if bold individuals suffer higher predation rates than shy individuals [28], then bolder individuals should be particularly likely to disperse to avoid predators while shy individuals would opt for a hiding strategy. Similar prediction can be made with activity/exploration levels because higher activity levels are often costly in environments of high predation risk [29–31]. Second, between-individual variation in sociability is likely to reflect different antipredator strategies. Social grouping is a known strategy to increase safety [32]. If social individuals thus have higher survival in the presence of predators than asocial ones, we expect asocial individuals to exhibit predator-induced dispersal. On the other hand, if social groups attract more predators [33], or if asocial individuals are more efficient at hiding or escaping predators, then asocial individuals might survive better than social individuals. In that case, social individuals should show predator-induced dispersal.

2. Material and methods

A thousand mosquitofish were transported from the Sacramento-Yolo Mosquito and Vector Control District to the Center for Aquatic Biology and Aquaculture (CABA), University of California, Davis in early April 2009 and held in groups of 60 in 80 l flow-through fibreglass tanks on a natural photoperiod (for early May, 14 L : 10 D cycle) at 22°C, and fed Tetramin flakes ad libitum and brine shrimp once a week. Mosquitofish were acclimated to these conditions for more than three weeks prior to behavioural observations, which were carried out between 21 April and 4 May, 18 May and 25 May, 13 July and 20 July, and 27 July and 3 August 2009 (four blocks).

Two weeks prior to behavioural observations, individual mosquitofish were marked with elastomer tags (Northwest Marine Technologies, Shaw Island, WA) 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. We checked for normal behaviour after marking by confirming that behaviour was similar between sets of unmarked and marked fish [16].

The evening 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. Around 35 fish were run through personality observations each day. We assayed a total of 560 fish over four periods of 4 days. We ran two behavioural assays to characterize behavioural types (BTs) and then their dispersal tendency was measured in artificial streams (see below). Because earlier work on the same population of mosquitofish showed that these BTs are significantly repeatable for at least four months (i.e. over much longer periods than necessary for the current study), we did not test for repeatability here [16,34].

(a) Tendency to shoal (sociability)

Following the methods from our previous studies [16,34,35], we recorded the amount of time spent near a shoal of conspecifics. 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) divided into three compartments (two small and one large centre compartment) using two transparent glass partitions 12.5 cm away from each side wall. One compartment held a stimulus shoal, while the other was left empty. The partitions allowed visual, but not physical or olfactory interaction between the shoal and the focal individual. We used six predetermined stimulus shoals, each comprising 14 randomly chosen mosquitofish (seven females and seven males). Although we did not assay or control for the personality types of the individuals in these shoals, using a relatively large shoal size ensured that shoals were all similar in average personality type. One of six predetermined stimulus shoals was introduced to one smaller compartment of each of six aquaria 1 h before 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 v. 2.01. The large compartment was divided with vertical marks every 3 cm; time spent shoaling was defined as time spent by the focal fish within the 3 cm closest to the stimulus shoal [36]. When the assay was complete, each individual was returned to its 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 [37,38]: 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 on 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 s).

During this assay, we recorded three behaviours (boldness, exploration and activity) and we added all of them, along with sociability, into a principal component analysis (see below). 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 [39], we follow several earlier papers (e.g. [9]). For small, schooling fish, a short latency to emerge alone from a dark refuge into an open, potentially dangerous, novel environment represents boldness, while exploratory tendency and activity are 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. However, as exploration and activity were measured in the same assay, these two behaviours were not entirely independent measures and it may induce correlations between them.

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.

At the end of each observation day, mosquitofish were weighed to the nearest 0.001 g. Each day, the 35 fish were distributed into four 80 l fibreglass tanks. The sex ratio was largely biased towards females in our sample (more than 85%), but we kept the sex ratio and density similar in the four tanks over the 4 days of behavioural observations. We chose this sex ratio because it was the sex ratio in the population of the vector control. After the 4 days of behavioural assays of each period, the four tanks contained 35 fish each. Three days after the end of the behavioural assays (except for the first set where fish were kept one week), these four groups were placed in four experimental streams for the dispersal assay (see below). This procedure was repeated for the four periods, creating overall 16 groups.

(c) Dispersal assay, density and predation treatments
The dispersal assay was conducted in four artificial streams at CABA, using the same basic methods as in our earlier study

[16]. 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 25.35 kW pump at the downstream end pumped water (370.7 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 the current. Each pool had three half flower pots 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).

For each trial, two days before dispersal assays, we added 60 unmarked fish in two of the four holding tanks. After adding 35 experimental fish, this created two high-density ($n = 95$) and two low-density groups ($n = 35$). Each population of fish was introduced into the most upstream pool, where a removable barrier at the outlet end kept the fish from dispersing, while still permitting water to flow into the riffle. In these upstream/release pools, we created two treatments of predation risk. Two populations (one of high and one of low density) were released in a pool with a caged trout. Trout were held in a screened enclosure (so mosquitofish got visual and chemical cues from trout) and three mosquitofish were released in the trout cage to allow alarm cues. The two remaining populations were released in pools with the screen enclosure containing only the three mosquitofish. 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. This procedure was repeated for the four periods, giving a total of 16 populations, four of each density × predation treatment. We allowed these fish to disperse for 24 h before capturing all individuals. The 24 h time span was chosen based on previous experiments, which showed that most fish that ultimately dispersed did so within 24 h.

(d) Statistics
We randomly distributed fish to the 16 populations over the four periods of time. For unclear reasons, one block unfortunately showed the following important differences from the other three blocks: (i) a much higher number of females that gave birth during behavioural assays (16 in that block versus five in the other three blocks combined); (ii) much lower average sociability and boldness scores; (iii) a 2.5-fold greater difference between populations in average boldness/sociability scores; and (iv) much lower average dispersal rates. In particular, the fact that this block exhibited lower sociability, lower boldness and lower dispersal potentially obscures our ability to detect causal relationships between these behaviours. Accordingly, we excluded this block and focused our analyses on the other three blocks. However, we checked that our results were similar when we used the fourth set.

Of the remaining 420 individuals (35 individuals/population, 12 populations), we excluded 14 from the analysis because of technical problems running boldness assays. Also, 13 individuals 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. Finally, we were unable to retrieve 21 individuals from the streams after dispersal assays. We did not include any of these individuals in the analyses. In total, 372 fish remained for analyses.

(i) Principal component analysis

Correlations between personality parameters (sociability, boldness, exploratory behaviour and activity) were tested with Spearman's rank correlations. Because our behavioural metrics were correlated (see Results), we performed a principal component analysis (PCA) with varimax rotation [40] in JMP v. 7 to define possible personality trait dimensions (see electronic supplementary material S1). Based on eigenvalues larger than 1, we identified two key PCA factors for further analyses [41]. Behaviours with a loading of at least 0.32 were considered to contribute to a component [42].

(ii) Dispersal decisions

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). We analysed the relationship between dispersal decisions and individual PCA scores using a mixed generalized linear model with a logit-link and a binomial error distribution in R v. 2.15.0, package lme4 [40,43]. The fixed effects were individual PCA scores, density and predation treatments, and the two-way interactions. We also included a random effect for the experimental population nested within the density and predation 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 [43,44]. The best-fitting models were selected from all possible models from the list of fixed effects (see above) using an information-based approach with Akaike's information criterion for small samples (AICc) [45]. 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). Total w was calculated as the cumulative weight of all models including a particular variable. The relative importance, the estimate and confidence intervals for variables were calculated from average supported models. All models with $\Delta < 2$ were considered to be supported [45]. Based on our results, we also ran a *post hoc* analysis using boldness and sociability scores instead of PCA scores (see electronic supplementary material S2). Indeed, boldness and sociability were not strongly correlated, which makes a problem of collinearity less likely and may allow study of the relative effects of the two behaviours [46].

3. Results

The four measured behaviours were significantly positively correlated to each other with the exception of a non-significant correlation between sociability and activity (table 1). From the PCA, we only retained two factors with eigenvalue exceeding 1.0. PC1 had strong component loadings for *exploration and activity*, PC2 represented *sociability and boldness* (see electronic supplementary material S1). Fish that had high PC1 scores explored a larger area and spent more time moving. Fish that had high scores on PC2 spent more time close to the shoal and took less time to emerge from the shelter.

For the dispersal decision analysis, four models were supported ($\Delta < 2$) while only two had $w > 10\%$ (table 2). All supported models had three predictors in common: sociability–boldness score (SB; total $w = 0.99$, relative importance on supported models = 1.00), predation treatment (P; total $w = 0.95$, relative importance on supported models = 1.00) and the interaction between sociability-boldness and predation treatment (SB * P; total $w = 0.86$, relative importance on supported models = 1.00). Three of the four supported models also included density treatment as predictor (D; total $w = 0.62$, relative importance on supported models = 0.64), with a higher

Table 1. Correlations between the four behaviours measured before the dispersal assay ($n = 502$). Correlation coefficients are given.

	boldness	exploratory behaviour	activity
sociability	0.16, $p = 0.002$	0.11, $p = 0.01$	0.06, $p = 0.19$
boldness		0.23, $p < 0.001$	0.21, $p < 0.001$
exploratory behaviour			0.73, $p < 0.001$

dispersal probability for the high-density treatment (estimate for low-density from averaged best models: -0.37, 95% CI: -0.84, 0.10). To better understand the sociability–boldness × predation treatment interaction, we ran separate analyses by predation treatment (table 3a,b). In the no-predation treatment, three models were supported ($\Delta < 2$) with $w > 10\%$ (table 3a). All three supported models had one predictor in common: sociability–boldness score (SB, total w and relative importance = 1.00). In the predation treatment, two models were supported while four models had $w > 10\%$ (table 3b). There was no consistency in the predictors among these models. A comparison of averaged estimates from these models (table 4) shows that asocial/shy individuals had a higher dispersal probability than more social/bolder individuals in the no-predation treatment while dispersal probability is unrelated to behavioural types in the predation treatment (figure 1).

We also ran a *post hoc* analysis with boldness and sociability scores instead of PC1 scores (see electronic supplementary material S2) to study the relative effects of the two behaviours. Nine models were supported ($\Delta < 2$) while only two had $w > 10\%$ (see electronic supplementary material, table S2). The best model had both the interaction between sociability and predation treatment and the interaction between boldness and predation treatment. In the nine supported models, four had the interaction between sociability and predation treatment (total $w = 0.45$, relative importance on supported models = 0.55) and six had the interaction between boldness and predation treatment (total $w = 0.49$, relative importance on supported models = 0.65). We ran separate analyses by predation treatment (see electronic supplementary material, table S3a and S3b). All supported models in the no-predation treatment had both sociability and boldness scores, while there was no consistency in the predictors among supported models from the predation treatment.

4. Discussion

(a) Personality-dependent dispersal and predation risk

Previous studies, conducted in the absence of predators, showed that dispersing mosquitofish have lower sociability scores than non-dispersing, resident fish. Individuals leaving the initial pool or moving further spent less time next to the shoal in earlier behavioural assays [16,34]. In these earlier studies, sociability and boldness scores could be teased apart in different PCA axes, and only sociability scores were related to dispersal tendency. In the present study, we found that in the no-predation-risk treatment, asocial/shy individuals were

Table 2. Selection of best models exploring dispersal decision in relation to density, predation treatments and individual behavioral types ($n = 372$). We report number of fitted parameters (k), Akaike's information criteria (AICc), model strength (Δ) and model weight (w). Supported models are in italic.

	candidate models[a]	k	AICc	Δ	w
1	$I + D + P + SB + P \times SB$	7	475.6	0	0.217
2	$I + P + SB + P \times SB$	6	475.6	0.05	0.211
3	$I + D + EA + P + SB + P \times SB$	8	477.5	1.97	0.081
4	$I + D + P + SB + D \times SB + P \times SB$	8	477.5	1.97	0.081
5	$I + P + EA + SB + P \times SB$	7	477.6	2.08	0.077
6	$I + D + P + EA + SB + D \times EA + P \times SB$	9	478.8	3.19	0.044

[a]In the models: I, intercept; D, density treatment; P, predation treatment; EA, individual exploration − activity score; SB, individual sociability − boldness score. Population random effect nested in density and predation treatments was in all models presented.

Table 3. (a) Selection of best models exploring dispersal decision in relation to density treatment and individual behavioral types for the no-predation treatment. (b) Selection of best models exploring dispersal decision in relation to density treatment and individual behavioral types for the predation treatment. We report number of fitted parameters (k), Akaike's information criteria (AICc), model strength (Δ) and model weight (w). Supported models are in italic.

	candidate models[a]	k	AICc	Δ	w
(a)					
1	$I + SB$	4	252.7	0	0.406
2	$I + D + SB$	5	254.1	1.36	0.205
3	$I + EA + SB$	5	254.6	1.83	0.162
5	$I + D + EA + SB$	6	255.9	3.17	0.083
(b)					
1	I	3	223.6	0	0.305
2	$I + D$	4	224.5	0.89	0.196
3	$I + EA$	4	225.7	2.05	0.110
4	$I + SB$	4	225.7	2.09	0.107
5	$I + D + EA$	5	226.6	2.99	0.068
6	$I + D + SB$	5	226.6	3.00	0.068

[a]In the models: I, intercept; D, density treatment; EA, individual exploration − activity score; SB, individual sociability − boldness score. Population random effect nested in density treatment was in all models presented.

Table 4. Parameter estimates from averaged models ($\Delta < 3$) of dispersal decisions in predation and no-predation treatments.

dispersal models[a]	parameter estimates $\pm$ s.e.[b]	95% CI
no-predation treatment	$SB = -0.60$	$-0.93, -0.26$
	$EA = -0.10$	$-0.40, 0.23$
	$D_L = -0.38$	$-1.19, 0.44$
predation treatment	$SB = 0.01$	$-0.31, 0.33$
	$EA = 0.03$	$-0.29, 0.35$
	$D_L = -0.36$	$-1.01, -0.29$

[a]In the models: D, density treatment; EA, individual exploration − activity score; SB, individual sociability − boldness score. Population random effect nested in density treatment was in all models presented.
[b]Subscript L indicates parameter value for low-density treatment.

more likely to disperse from their initial pool than more social/bold conspecifics. In the *post hoc* analysis, we tried to separate the effects of boldness and sociability. This analysis suggests that both boldness and sociability affect dispersal tendency. However, supported models have sociability and/or boldness as predictors of dispersal tendency, and the two behaviours are correlated. We believe that the effects of boldness and sociability could not be clearly separated, and we cannot rule out the possibility that dispersers were shyer, and not just more asocial, than residents.

Based on some earlier studies, we also expected that asocial individuals should disperse more from high-density populations while social individuals should disperse more when densities are low [5,6]. However, here, sociability-

dependent dispersal was not a function of population density; in particular, social fish did not tend to disperse more than asocial fish at our lower density. A plausible explanation is that even our 'low-density' treatment was not low enough to induce social individuals to disperse to find higher densities.

For invasive species, personality-dependent dispersal can have important consequences because it means that individuals at the front of an invasion are not a random subset of the source population, but display specific behavioural characteristics. This could result in higher invasion success, as already shown in other species [8], and can hasten the spread of an invasion [47]. Here, we corroborated previous studies on this invasive mosquitofish in showing that dispersers tend to be more asocial than average. How might asocial individuals fare in novel habitats? We recently showed that at low density (as might often be the case with new colonization events) asocial individuals are also more likely to escape novel predators [48]. At low density, it might be better to be asocial because small shoals attract more predators than isolated individuals and provide limited protection [33]. A low shoaling tendency by dispersers might therefore increase resistance against novel predators and thus enhance settlement success at the invasion front.

Interestingly, predation risk in the resident habitat modified the pattern of personality-dependent dispersal. With a caged predator in the initial pool, personality traits of individuals leaving were no different from residents. Personality-dependent
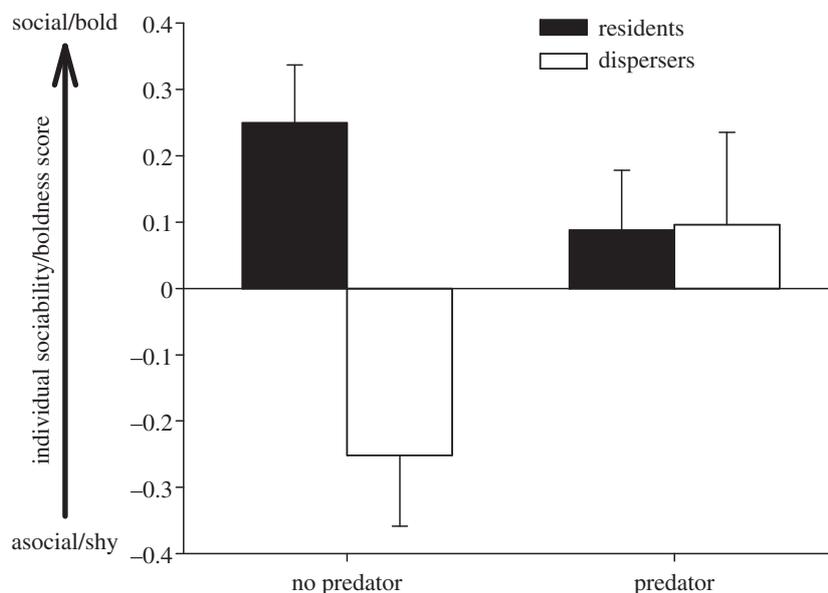
Figure 1. Mean individual sociability/boldness value in relation to dispersal status in the no-predation and predation treatments. Shown are mean values ($\pm$ s.e.) of the sociability score as a function of the dispersal status (residents = individuals that stayed in pool 1; dispersers = individuals that left pool 1).
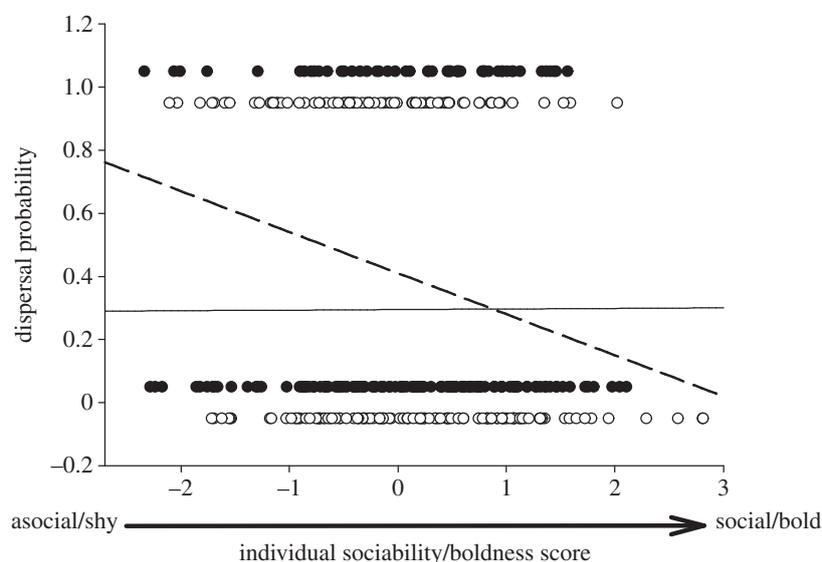

Figure 2. Individual dispersal status in relation to individual sociability/boldness value in the no-predation (open circle, dashed line) and predation (filled circle, solid line) treatments. Shown are individual values of the dispersal status (residents = 0; dispersers = 1) as a function of sociability and associated predicted lines.

dispersal is therefore negated under risk of predation. Figure 2 (compare the dashed and solid lines) suggests that this was due to two personality-dependent responses to risk: (i) asocial/shy individuals dispersed less in the presence versus absence of predation risk, while in contrast (ii) social/bold individuals dispersed more in the presence versus absence of enhanced risk. The fact that predation risk caused some prey to increase their dispersal tendency while others decreased it has often been seen in stream ecology [24,49]. The usual explanation for why prey increase their dispersal in response to risk is straightforward: dispersal is a form of predator avoidance. Fish that are bold (and social) might be under particularly high risk of predation if they stay in the pool with predators, and thus have particularly strong incentives to disperse. In contrast, the classic explanation for why prey might exhibit reduced dispersal in the face of predation risk hinges on the risk of the act of dispersing per se [24]. If it is very high (e.g. if prey must be

active in open water to move across a pool and disperse), prey (particularly 'fearful' prey) often reduce activity, hide more and thus disperse less. This could be what more shy/asocial fish did. Previous work on predation risk and dispersal showed contrasting dispersal responses by different prey species [24,49]. With the rise of the study of individual differences within species, it is interesting to see parallel personality-dependent differences within species.

(b) Behavioural syndrome

Consistent with our previous studies [16,34], we found positive correlations between four personality traits—sociability, boldness, exploration and activity—with the exception of the correlation between sociability and activity. Boldness, exploration and activity were, however, measured in the same assay and thus could be argued to be not entirely independent

measures. In particular, because exploration and activity were measured during the same 5 min after emergence, it is not surprising that these two behaviours were highly correlated ($r = 0.73$). Boldness, however, was measured before exploration and activity, and was only weakly correlated to the other two behaviours ($r = 0.21-0.23$).

In contrast, sociability was measured in a separate assay from the other three behaviours. Individuals emerging sooner from a refuge into a novel environment also tend to shoal more. This result is reinforced by our principal component analysis, where boldness and sociability grouped together on the same PC axis. This association between sociability and boldness is quite surprising as it is often thought that shoaling is a protection against predators [50,51], and therefore shy individuals should shoal more. However, a similar positive relationship between boldness and shoaling/social tendency has been observed in three-spined stickleback [36,52,53] and in guppy [54]. One explanation can be derived from the cost–benefit balance of shoaling. Shoaling protects against predators through a dilution effect, earlier predator detection or predator confusion, but predators may attack groups more frequently than solitary individuals because groups are more easily detected [33,51,55]. Social context is thus believed to facilitate risk-taking behaviours, with individuals becoming bolder in the presence of conspecifics [56–59]. For example, Ward [58] showed that focal individuals in larger shoals emerge sooner from refuges and explore novel environments more. However, the shyest individuals might not be able to afford this risky shoaling behaviour and might opt for a strategy consisting of staying in refuges and periodically leaving to feed instead of swimming with a shoal for longer periods. This would match our previous results on shoaling behaviour of asocial individuals [35]. We found that asocial individuals spend most of their time far from any shoals and are less choosy regarding shoal characteristics. It thus seems that social individuals are more consistent in their shoaling tendency and shoal choice while asocial individuals periodically join shoals when needed (for food or mates). Under this hypothesis, we could thus expect the shyest individuals to stay far from shoals, for example in refuges (our metric of boldness), and the moderately bold and the boldest individuals, followers and leaders of shoals, respectively, could form shoals because they can afford to take the risk of swimming and thus being exposed for longer periods of time. The relationship between sociability and boldness found here would thus be driven by individuals with the lowest scores of boldness.

Another explanation might be that social individuals were in larger groups prior to the experiment, which might have lasting consequences on their boldness scores. However, the consistency of boldness over four months and across various social contexts does not support this explanation [34]. Finally, it is also possible that social fish are searching for others during our boldness assay and that it forces them to exit refuges more quickly to find a shoal. This would suggest that social tendency can heavily influence observed boldness scores when such behaviour is measured alone. Further experiments measuring boldness of the same individuals when alone and when in groups are needed to better understand this boldness–sociability syndrome.

5. Conclusion

Recent papers have noted substantial interest in the possible importance of personality-dependent dispersal in ecological invasions, and spatial ecology in general [13,16,47,60]. Experimental studies have concluded that, depending on the system, dispersers tend to be bolder, more aggressive, faster explorers or less social than non-dispersers [5]. However, with the exception of one study [6], personality-dependent dispersal has not been studied in contrasting environments (e.g. high versus low density, predation versus no predation risk, high versus low food availability). In the overall study of dispersal, the clear consensus is that both phenotypic traits and ecological contexts are involved in dispersal decisions from departure to settlement [3,61]. As the phenotype of individuals drives both their reaction to and success in coping with biotic and abiotic characteristics of their environment, adaptive dispersal decisions should commonly depend on interactions between phenotypes and ecological contexts. Here, we indeed found that the relationship between personality traits and dispersal inclination differs depending on ecological contexts. We invite future studies to further examine how personality-dependent dispersal is affected in varying environments.

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