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The eco-evo-devo of stickleback personalities

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Effects of personality and social context on movement tendencies in three-spined sticklebacks

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ABSTRACT

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Assessing social effects on individual behaviour is challenging because knowledge of an individual's social environment is often difficult to gain, especially for animals which form dynamic social groups. We here report on an experiment where the social environment could be manipulated. To this end, we capitalised on the availability of populations of migrant and resident sticklebacks (*Gasterosteus aculeatus*) that exhibit strong differences in movement tendencies. This allowed us to create mixed shoals with different proportions of migrants and residents, to investigate the occurrence of social effects between migrant and resident fish. In a mesocosm consisting of linearly connected ponds, we found that the overall movement patterns, as quantified by the number of pond transitions, remained consistently higher in migrants than in residents, regardless of the social group composition. The fish's intrinsic movement tendency was the main predictor of the observed variation between populations. However, at the start of the experiment, when social effects were expected to be strongest, residents were more likely to leave the starting pond in the presence of migrants than in their absence. As this increase in movement tendency was not related to the frequency of migrants in the mixed groups it cannot solely be ascribed to social conformity. Additionally, we found an effect of being part of the majority on movement: the first fish to leave the starting pond was almost always a member of the majority group (be it migrants or residents). In conclusion, we found little evidence for social modulation of movement based on differences in the populations' movement tendencies, but rather an effect of being in a majority group.

3.1 INTRODUCTION

Many animals live in groups for at least part of their lives. Group living can reduce predation risks due to group vigilance (Dall et al., 2005; Ward et al., 2011), predator confusion (Jeschke and Tollrian, 2007; Treherne and Foster, 1982), or risk dilution (Foster and Treherne, 1981; Hamilton, 1971; Lehtonen and Jaatinen, 2016). Individuals in social groups may also profit from social learning (Snijders et al., 2021), collective decision-making (Couzin et al., 2005), and improved locomotion performance (e.g. in fish, Marras et al. (2015); in birds, Lissaman and Shollenberger (1970)). Group living can also be costly, for example due to increased competition, but in many cases the benefits outweigh the costs.

Social groups are made up of individuals and individuals typically show stable inter-individual differences in behaviour ('animal personality'). While behavioural consistency, one of the hallmarks of animal personality, may arise from repeated social interactions (Dingemanse and Araya-Ajoy, 2015; Wolf and Weissing, 2010), particularly during critical periods of development (e.g., Fischer et al. (2017)), social environments are rarely stable during an individual's lifetime. Thus, as animals grow and adjust to a particular social environment, they may later in life need to either maintain themselves in similar social environments that match their personality ('social niche choice'; Bergmüller and Taborsky (2010); Montiglio et al. (2013), or modify their personality to match that of their interaction partners ('social modulation of behaviour') (Van Den Bos et al., 2013; Webster and Ward, 2011).

Social modulation of behaviour often takes the form of conformity, where individuals adopt the behaviour of their social group. Such conformity can for example help to avoid predation oddity effects, where predators preferentially prey on individuals that differ from their group mates (Landeau and Terborgh, 1986; Theodorakis, 1989). For example, in three-spined sticklebacks (*Gasterosteus aculeatus*), individuals choose to forage on suboptimal patches by staying within a larger shoal even when they know the patch to be of lower quality (Webster and Ward, 2011). Shy sticklebacks also spend more time out of cover in the presence of a bold than a shy partner, thus behaving more like their social partner (Jolles et al., 2014). In the collared flycatcher (*Ficedula albicollis*), birds arriving later at a breeding site often copy the nesting site choices of early-arriving birds (Jaakkonen et al., 2013).

One challenge when studying social modulation of animal behaviour is that detailed knowledge of an individual's social environment is often difficult to gain. Ideally, one would not only need data on the behaviour of the

focal individual but also on the behaviours of all individuals it interacts with, information that is hard to obtain for animals that form dynamic social groups. Another difficulty lies in the reciprocal causality of social interactions, where the behaviour of a focal individual can either elicit a certain behaviour in an interacting partner or be elicited by the partner's behaviour (Dingemanse and Araya-Ajoy, 2015). Because of these challenges, studies on social conformity typically compare an individual's behaviour in isolation vs in a social group or before and after (repeated) social interactions. While these approaches offer valuable insights, interpreting the outcome can be difficult. For example, measurements of an individual's performance in isolation and subsequently in a social group may capture different behaviours. For social organisms, behaviour measured in isolation may actually reflect responses to a novel situation or stress (Ramesh et al., 2021). Similarly, a change in an individual's behaviour in a group compared to in isolation may indicate a preference for using social information over personal information.

A promising approach to overcome these challenges is to repeatedly collect (longitudinal) behavioural data of individuals in groups with a standardised composition. Here we report on such an approach. To assess the role of social effects in the movement behaviour of three-spined sticklebacks, we make use of conspicuous differences in movement behaviour. We have shown previously that the members of two stickleback populations ('migrants' and 'residents') 1) differ in average movement tendencies in a mesocosm, with migratory individuals moving much more than residents and 2) show high repeatability in this behaviour (Ramesh et al., 2021, 2023). By manipulating group composition, i.e., varying the proportions of residents and migrants, and collecting individuals' movement behaviour repeatedly in these different social groups we investigated whether individuals adjusted their behaviour according to the social context. We studied mixed groups of 10 fish each in a mesocosm – a system of 5 connected semi-natural ponds where the movements of individual fish can be tracked remotely (Ramesh et al., 2022) (Fig. 3.2)– and collected longitudinal movement behaviour of individuals over a period of 16h. Figure 3.1 illustrates four (non-exclusive) hypotheses through which social modulation may affect individual movement tendencies: **a)** No effect: migrant and resident sticklebacks do not modulate their movement tendencies in response to social group composition. **b)** Social conformism: individuals in a group conform to the behaviour of the majority, such that e.g., residents placed in a majority migrant group would display behaviour similar to that of migrants (and vice versa). **c)** Averaging effect: To maintain group coherence, all individuals in a group adjust their behaviour to some extent, such that we

observe an averaging effect. **d)** Differential responsiveness: either migrants or residents respond by changing their movement tendencies to match that of the others (e.g., Guayasamin et al. (2017)).

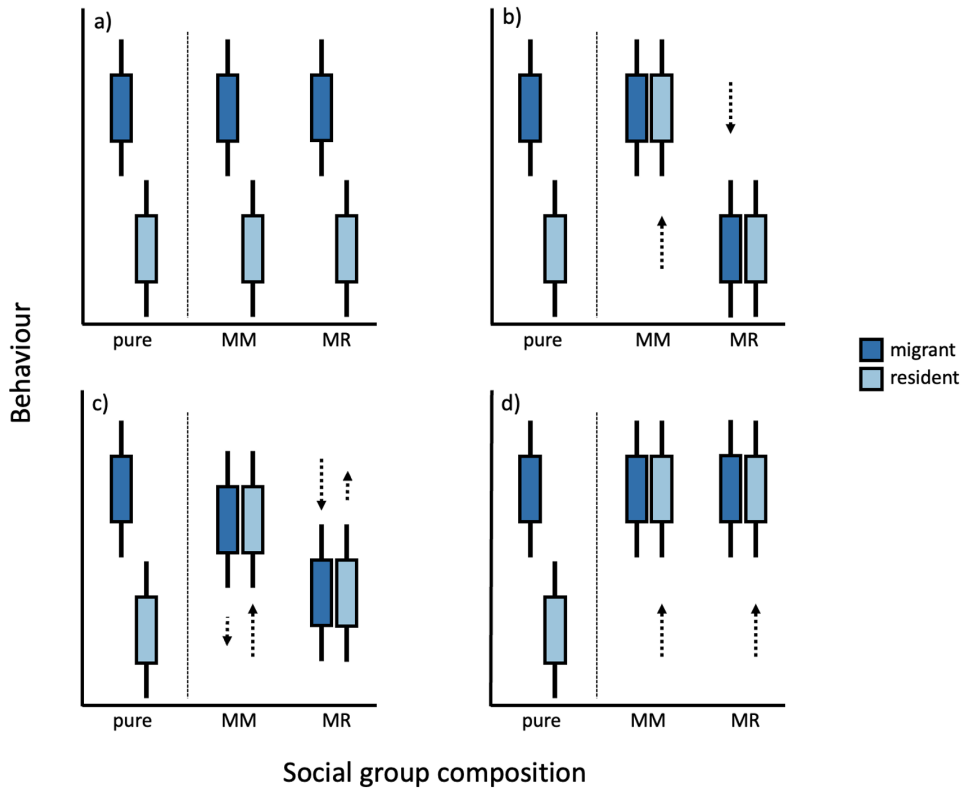


Figure 3.1 | Four potential scenarios for the social modulation of individual movement tendencies. (a) No effect. In the absence of social modulation, migrants have a consistently higher movement tendency than residents. (b) Social conformism. If individuals conform to the behaviour of the majority in their group, minority individuals will adjust their movement behaviour to that of the majority in their group. (c) Averaging effect. If all individuals adjust their behaviour to that of their group members, an averaging of movement tendencies is to be expected, where the resulting movement rate is closer to the movement rates of the majority in the group. (d) Differences in responsiveness. When migrants and residents differ in responsiveness, the effect of social modulation may be asymmetric. This is illustrated for the case that residents are responsive while migrants are unresponsive: here, only residents adjust their movement to that of the majority, and not vice versa. Pure: group of residents or migrants. MR: group with a majority of residents (7 residents + 3 migrants); MM: group with a majority of migrants (3 residents + 7 migrants). Arrows indicate change in movement tendencies as a result of social modulation. Adapted from Webster and Ward (2011).

3.2 METHODS

3.2.1 STUDY POPULATIONS

We used the same fish as in Ramesh et al. (2023). The fish were caught between March and April 2020 from two populations in the northeast of the Netherlands. These two populations have become separated due to water management efforts undertaken 50-60 years ago. Migratory sticklebacks, that move inland in spring in order to breed in freshwater were caught during inland migration at the mouth of a river ('NSTZ': 53013'54.49", 7012'30.99"), whereas resident sticklebacks were caught close by in a sidearm of another river that is permanently closed-off from the sea ('LL-A': 53017'56.14", 702'1.28"). For the purpose of individual identification and monitoring using a RFID ('Radio-frequency Identification') system all fish were anaesthetised using MS-222 (0.3 g/l) and injected with a PIT tag (ID-100A/1.4 Mini Transponder (8mm); Trovan, Ltd., Santa Barbara, California) into the abdominal cavity in the previous study following Cousin et al. (2012) (more details in 'Ethical Note'). Each fish thus carried an individually identifiable tag that can be remotely detected with PIT antennas. Prior to testing, all fish were given at least 10 days to recover from the procedure in 100L housing ponds outside. Fish were fed brine shrimp and red bloodworms (3F Frozen Fish Food by, The Netherlands) *ad libitum* daily.

3.2.2 EXPERIMENTAL GROUPS

In the previous experiment, the same fish were tested in a row of connected ponds ('mesocosm', Fig. 3.2) in 'pure' groups of either 10 migrant or 10 resident fish. There we found that individuals consistently differed in between-pond movement over several days (i.e., were repeatable; adjusted R (95% CI) = 0.42 (0.34, 0.51)), and that residents consistently moved less than migrants (Ramesh et al., 2023). We used the individual behavioural data observed in these pure groups as a standard of comparison (baseline) for the movement in mixed groups observed in the current study. We here tested for social modulation by manipulating the animals' social environment. We created two mixed treatment groups consisting of a majority of residents ('MR': 7 residents + 3 migrants) or a majority of migrants ('MM': 3 residents + 7 migrants). First, fish were randomly assigned to one of the two treatments regardless of their own origin (for example, first MR or MM). Next, the same fish were re-tested in the opposite treatment (for example, if the first test was in MR, the second test was in MM and vice versa). As a result, all individuals were tested in all treatments (i.e., three tests per fish: 'pure'

group in Ramesh et al. (2023); MR and MM in the present study). Tests took place between 19.04.2020 and 22.05.2020 and one MR and one MM group were always tested on the same day to homogenise the effects of e.g., weather. The vast majority of fish ($\approx 80\%$) was tested in mixed groups 6-10 days after being tested in pure groups. Due to the loss of PIT tags and some mortality, not all fish were ultimately tested in all three groups. In total, we tested 60 residents and 49 migrants in six and five pure groups, respectively, and 52 residents and 50 migrants in 18 MM groups, and 58 residents and 48 migrants in 17 MR groups. In order to test each fish in minority (i.e., residents in MM and migrants in MR), some fish had to be tested more than three times (i.e., some residents were repeatedly tested in MR and some migrants were repeatedly tested in MM). To keep sample sizes even between the treatments and to avoid issues arising from overt habituation to the experiment, we only considered each individual's first test in each of the three experimental groups in the statistical analyses. Due to PIT tag loss, some test groups consisted of only 9 individuals, while some consisted of 11.

Between tests, fish were kept according to their population of origin in groups of 30 individuals in smaller holding ponds (100 L filled with natural freshwater) outdoors and were given a minimum of 2 days between behavioural tests. Experimental groups of 10 fish each were created 24h prior to testing and kept in separate holding ponds during the acclimatisation period. On the morning of testing (10 a.m.) a group of 10 fish was gently released into the first pond in a row of five connected ponds. Connecting tubes were closed off during the first five hours of the experiment so that fish were confined to pond 1 to monitor within-pond movement, after which the connection to the other ponds was opened to record between-ponds movement.

For each of the experimental rounds, we monitored within-pond and between-ponds movements (see 'Monitoring between-ponds movement', Fig. 3.2 and Fig. A1). Because we did not find any differences between migrants and residents in terms of within-pond movement in our previous study on pure groups ('baseline'; Ramesh et al. (2023)), and hence did not expect social effects to act here, we focused on between-ponds movements in the present study. However, see Figure A2 for a comparison of within-pond movement between migrants and residents.

3.2.3 THE MESOCOSM

The mesocosm, as depicted in Figure 3.2, consisted of a row of five connected ponds (each 1.6m diameter; 1200L; connected with tubes of 11 cm diameter).

Ponds were fitted with circular RFID antennas (11cm diameter) to remotely monitor movements within the first pond (Fig. A1) and between ponds (see below and Fig. 3.2). The system was supplied with freshwater from a nearby water body, similar to natural stickleback habitats in the Netherlands (see details in Ramesh et al. (2022)).

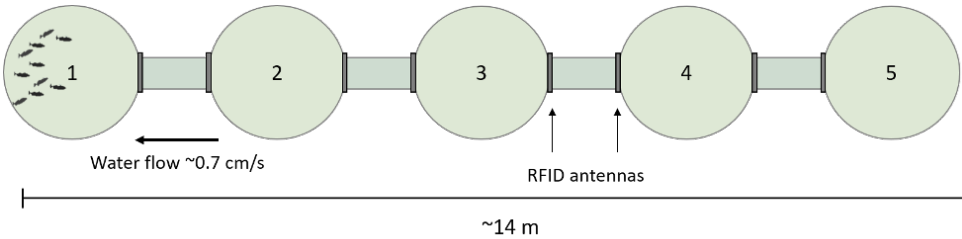


Figure 3.2 | Illustration of the mesocosm setup. The mesocosm setup of connected ponds was used to assess the movement of sticklebacks. A mixed group consisting of 10 sticklebacks was introduced in the first pond as shown. All corridors were fitted with RFID antennas on both ends to assess the movement and the direction of movement of individual fish.

3.2.4 MONITORING BETWEEN-PONDS MOVEMENT

Five hours after the start of the experiment we gently removed all RFID antennas used to monitor movement within the first pond. A pump connected to the nearby water body was started, creating a flow from the last pond toward the starting pond, mimicking conditions of upstream migration during spring (Fig. 3.2). Fish were given 30 minutes to recover from the disturbance caused by removing the antennas; then the connection of pond 1 to the other ponds was gently opened and we recorded the fish's movement between ponds for the next 16.5h (3.30 p.m. - 8 a.m.). Specifically, we monitored each fish's latency to exit the first pond (i.e., time in hours to enter the second pond) and the number of transitions from one pond to another – regardless of direction (i.e., back-and-forth transitions count the same as consecutive transitions in one direction). After the experiment, the fish were returned to holding groups according to their origin.

3.2.5 ETHICAL NOTE

Housing and testing of behaviours were in adherence to the project permit from the Central Committee on Animal Experiments (CCD, the Netherlands) under the licence number AVD1050020174084. In our previous study, we did not observe any detectable changes in behaviour of PIT tagged individuals and mortality within the first week after the procedure –when the risk for

e.g., infections is highest– was very low ($< 1\%$) (Ramesh et al., 2023). During the experiment, fish were housed and tested for behaviours outside and under natural light and weather conditions in water from a nearby water body that is typical for stickleback habitats in the Netherlands. Hence, throughout the experiment, fish experienced conditions resembling stickleback habitats in the wild. In total 10 resident (out of 86 initially caught) and 6 migrant fish (out of 62 caught) died over the course of the summer that we performed the experiments. Wild sticklebacks in our population typically die after about a year, so some natural mortality over the course of the summer was expected.

3.2.6 STATISTICAL ANALYSIS

Our aim was to test whether social group composition affected individual movement tendencies as quantified by the tendency to exit the first pond and the number of transitions between ponds. The tendency to exit the first pond was quantified by two parameters: the probability to leave the first pond and the latency to leave the first pond. Preliminary analyses showed that fish exhibited very little variation in their latency to leave the first pond. They either never left at all, or very quickly (of the fish that left the first pond, 95% left within the first 5 hours). For statistical analysis, we therefore did not analyse latency time but instead classified the fish as ‘leavers’ and ‘non-leavers’ and tested whether the probability to leave the first pond was affected by social group composition. We conducted a more fine-grained graphical analysis on the latency to exit the first pond.

All analyses were conducted with R (v4.2.2; Team (2020)) in the RStudio IDE (v1.2.5019). Variation in the probability of fish to leave the first pond and in between-pond transitions were analysed separately in Bayesian univariate response models using the brms package (v2.18.0; Bürkner (2017, 2018, 2021) where treatment (‘pure’ (baseline), ‘MM’ or ‘MR’ – to test the effect of social environment), origin (‘resident’ or ‘migrant’ – to test if residents and migrants differ in their responses) and treatment \times origin (to test for differential responses of residents and migrants to the treatment) were included as fixed factors, and individual ID and test group ID as random effects. An observation-level random effect (‘obs’) was added to control for overdispersion (OLRE, Harrison, 2014) which was detected using the ‘DHARMa’ package (Hartig, 2022). Pairwise contrasts between the different treatments (social groups) and between origins, were conducted using the ‘emmeans’ package (v1.8.2, Lenth (2018)) and reported in the supplementary materials (Tables A1 & A2).

The odds ratio of leaving/not-leaving the first pond was assumed to result from a Bernoulli distribution and modelled with a ‘logit’ link function, while the number of pond transitions was assumed to result from a Poisson distribution and modelled with a ‘log’ link function. For population-level (‘fixed’) effects, we used ‘weakly informative’ Gaussian priors (mean = 0, SD = 1) (Lemoine, 2019). For group-level (‘random’) effects, we used the default priors of brms (half-t density with 3 degrees of freedom) for standard deviations. Models were run with their chosen families and with and without correction for overdispersion (OLRE, Harrison (2014)). Final models including correction for overdispersion were chosen based on best fit using waic (Vehtari et al., 2017; Watanabe and Opper, 2010). For each model, we ran four chains with 1000 discarded warmup iterations, followed by 3000 sampling iterations, thus yielding 12000 posterior samples per model. Trace plots were used to monitor proper mixing of chains. Convergence of chains was ensured by verifying that \hat{R} values were close to 1.00. Model fits were evaluated by inspecting posterior predictive checks, using the `pp_check()` function of brms. Estimates of fixed effects (β) and standard deviation of random effects are given with their Bayesian credible intervals (C.I.).

3.3 RESULTS

3.3.1 PROBABILITY TO LEAVE THE FIRST POND

The probability of leaving the first pond was consistently high in migrants, irrespective of the social context (proportion migrant leavers: pure = 0.76; MM = 0.74; MR = 0.75), while the leaving probability in residents was higher (and comparable to that of the migrants) when in a mixed group than in their pure (baseline) group (proportion resident leavers in pure groups = 0.45; MM = 0.81; MR = 0.72), suggesting that the effect of the social environment on the probability to exit the first pond differed between migrants and residents (Fig. 3.3a). The visual impression is confirmed by the Bayesian response model in Table 3.1 (strong effect of ‘treatment x origin’ (treatment–MR \times origin–resident & treatment–MM \times origin–resident)), and the post hoc tests in Table A1.

3.3.2 POND TRANSITIONS

The median number of pond transitions was substantially larger in migrants (16 in pure groups, 21 in MM, and 23 in MR) than in residents (0 in pure groups, 4 in MR, 4.5 in MM) in all social group settings, showing that the

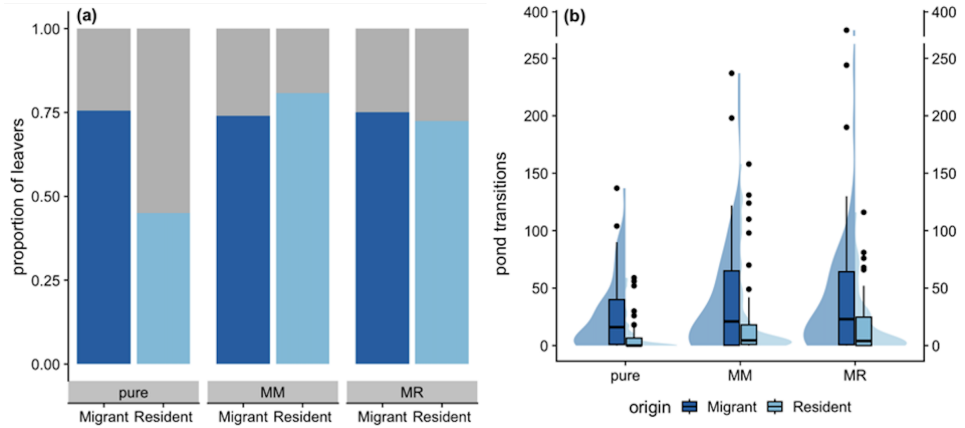


Figure 3.3 | Movement behaviour in the mesocosm. (a) Proportion of migrants (dark blue) and residents (light blue) that left the first pond within the first hour in each type of social group. (b) Number of pond transitions in each type of social group for migrants and residents. Boxes show the median with 25th and 75th percentiles. Whiskers indicate values within 1.5 times the interquartile range, and circles represent values outside this range. Shaded density kernels represent the frequency and distribution of raw data points. Only individuals' first test in each experimental group is displayed. Pure: group of residents or migrants. MR: group with a majority of residents (7 residents + 3 migrants); MM: group with a majority of migrants (3 residents + 7 migrants).

composition of the social group had only a small effect on the number of pond transitions in both migrants and residents (Fig. 3.3b). Both types of fish moved slightly more in mixed groups than in their corresponding pure group, but these differences were relatively small. These conclusions are confirmed by the statistical analysis in Table 3.1 (credible negative effect of 'origin– (resident, pure)' & absence of a credible effect of 'treatment' (neither of treatment–MR, nor of treatment–MM) on the number of pond transitions in Table 3.1). For post-hoc tests see Table A2.

3.3.3 SOCIAL DYNAMICS IN LEAVING THE FIRST POND

To shed light on the potential mechanisms that underlie animals' decisions to leave the first pond, we take a closer look into the timing of when individuals left the first pond. This helps to identify, for example, whether fish moved alone or in groups (and with whom) and to uncover social effects such as leader-follower dynamics. In Figure 3.4 we plotted the individual latencies to leave the first pond within the first hour after opening the connection from the first pond.

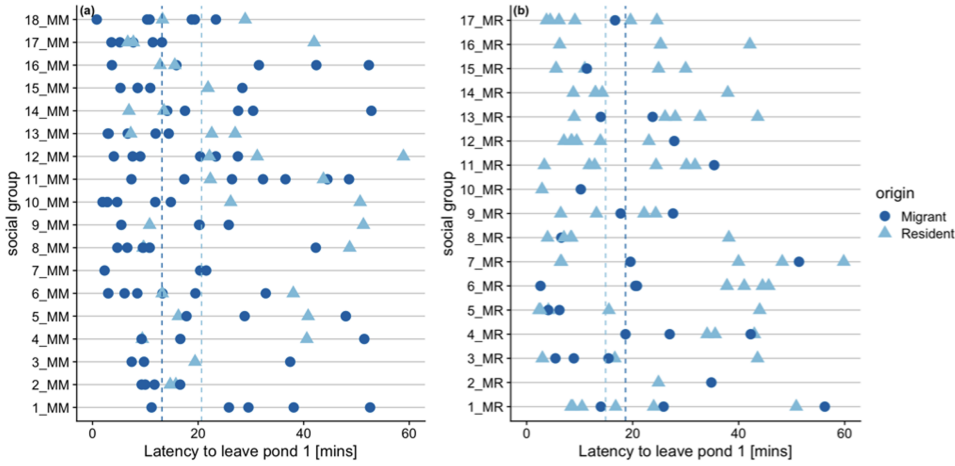


Figure 3.4 | Individual latencies to leave the first pond in mixed social groups. (a) Individual latencies within the first hour after opening the connection from the starting pond in groups with a majority of migrants. (b) Individual latencies within the first hour in groups with a majority of residents. Dashed lines indicate the median latency for migrants (dark blue) and residents (light blue), respectively.

Table 3.1 | Bayesian univariate response models of the probability to exit pond 1 and the number of pond transitions. Estimates of fixed effects (β) and standard deviation of random effects are given with their Bayesian 95% credible intervals (C.I.). Estimates with a 95% C.I. that do not include 0 are indicated in bold.

	Probability to exit pond 1	Number of pond transitions
Fixed effects	β (95% C.I.)	β (95% C.I.)
intercept– (migrant, pure)	6.86 (1.41, 16.64)	1.95 (0.90, 3.00)
treatment–MR	-0.31 (-6.72, 6.03)	0.36 (-0.76, 1.46)
treatment–MM	0.52 (-6.04, 7.49)	0.35 (-0.76, 1.52)
origin– (resident, pure)	-8.64 (-21.36, -1.59)	-2.10 (-3.55, -0.67)
treatment–MR \times origin–resident	7.07 (-0.61, 19.81)	0.88 (-0.54, 2.31)
treatment–MM \times origin–resident	9.62 (1.08, 24.79)	1.25 (-0.23, 2.71)
Random effects	SD (95% C.I.)	SD (95% C.I.)
obs	6.25 (1.77, 14.39)	1.36 (1.16, 1.59)
individual ID	7.36 (2.85, 16.09)	1.75 (1.41, 2.15)
group ID	3.18 (0.47, 7.50)	0.89 (0.56, 1.27)

Figure 3.4 shows that fish, to a large part, left the first pond alone rather than in a group. The mean time between two subsequent fish leaving the

first pond within the first hour across all experimental groups is 6.5 minutes (SD= 2.4). Individual latency values of fish leaving the pond are thus in most cases separated by several minutes, even when looking only at the first full hour after opening the connection to the other ponds (in which 80% of all ‘leavers’ exited the first pond).

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In both mixed group treatments, fish from the majority group left the first pond faster than fish from the minority group. In fact, the median time to leave pond 1 in the MM setting was shorter in migrants than in residents (13.2 minutes versus 20.7 minutes), while in the MR setting, the median time was shorter in residents than in migrants (14.9 minutes versus 18.7 minutes). In line with these results, a fish from the majority group (i.e., a migrant in Fig. 3.4a and a resident in Fig. 3.4b) left pond 1 first in 31 of the 35 experimental runs. This outcome would be very unlikely if the fish had a fixed leaving tendency, irrespective of the social context. To show this, let us assume the opposite: all fish have a fixed leaving tendency, and in mixed groups, the leaving tendency of residents is the same as the leaving tendency of migrants (as suggested by Fig. 3.3a). On the basis of this null hypothesis, the probability that in a given experimental run a member of the minority group leaves first is 0.3 (as 3 of the 10 fish belong to the minority group). The probability that a member of the minority group leaves first in k out of N trials is given by the binomial $B(k; N, 0.3) = \frac{N!}{k!(N-k)!} \cdot 0.3^k \cdot 0.7^{N-k}$. In view of Fig. 3.4, 4 minority fish (two instances in MM and two instances in MR) were the first to leave pond 1 in a total of 35 trials. On the basis of the null hypothesis, the probability that a minority fish leaves first in 4 (or fewer) of the 35 trials is thus given by: $B(0;35,0.3) + B(1;35,0.3) + B(2;35,0.3) + B(3;35,0.3) + B(4;35,0.3) = 0.0091$, implying that the null hypothesis can be rejected with high confidence.

3.4 DISCUSSION

In this study, we investigated whether individuals belonging to a migratory and a resident (non-migratory) population, which differ considerably in movement behaviour, adjust their behaviour to their social group. Using a mesocosm consisting of connected ponds, our results show that in mixed population groups individual sticklebacks maintain their larger-scale movement tendencies—with migrants moving more between ponds than residents—irrespective of changes to their social environment. Residents however showed some degree of plasticity: they were more likely to exit the first pond in mixed groups than in pure resident groups. At face value, the data on movement between

ponds (Fig. 3.3b) are in line with the “no social modulation” hypothesis (Fig. 3.1a), while the pond 1 exit data (Fig. 3.3a) are largely in line with the “differential responsiveness” hypothesis (Fig. 3.1d). Moreover, the more detailed individual-level data of Fig. 3.4 provide evidence that another aspect of movement (i.e., the latency to leave the first pond) may have been, in migrants and residents, affected by being in a majority group, a modulating effect of the social context we initially did not anticipate. However, as discussed later, alternative explanations for the patterns found cannot completely be ruled out.

We found that the proportion of resident leavers in mixed social groups increased to a level comparable to that of migrants. Residents may have thus responded to changes in their social environment, by following migrants out of the first pond. Alternatively, but not mutually exclusive, residents may have (more indirectly) reacted to a rapid decrease in the number of individuals in the starting pond caused by migrants leaving. The latter mechanism is more unlikely in the majority resident groups with only few migrants. Interestingly, residents were not only more likely to exit the first pond in the majority migrant groups but also in the majority resident groups compared to pure resident groups. Our analysis of individual latency times (Fig. 3.4) shows that leader-follower effects are unlikely to have driven our results. In all except two majority resident groups, we found that it was a resident individual (and not a more mobile migrant) that initiated movement out of the first pond (Fig. 3.4b). Furthermore, in many cases, several residents left the starting pond before even the first migrant did. Both findings indicate that it is unlikely that social conformity played a role in the residents’ behaviour, at least in majority resident groups. In majority migrant groups, a leader-follower explanation cannot be ruled out.

Due to logistical constraints, all fish were tested in mixed groups only after having previously been tested in their respective pure groups. As a result, the fish in the mixed-group setting were already somewhat familiar with the experimental setup. In the appendix (Figure A3 and Table A3), we provide evidence that familiarity with the experimental setting does indeed affect the movement behaviour in the mesocosm: the movement tendencies of both resident and migrant fish tended to increase with the number of tests the fish had been involved in. Such habituation to the experimental setup is often seen when individuals are repeatedly tested in the same environment: behaviours are initiated sooner or expressed to a greater extent (Finger et al., 2016; Magnhagen and Staffan, 2005). In our statistical analyses, we only included the data of an individual’s first use in a mixed-group setting. However,

we cannot rule out the possibility that the residents' increased probability of leaving the first pond in a mixed-group context (when compared to the pure-group setting) predominantly reflects increased familiarity with the experimental set-up.

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We do not have an obvious explanation for the finding that in almost all experiments a fish of the majority group was the first to exit the starting pond. One might speculate that majority fish are more inclined to leave the starting pond in order to avoid competition from similar individuals, resembling density effects in dispersal decisions or during foraging (Bowler and Benton, 2005; Michelena et al., 2010). However, there are other explanations as well, which are based on familiarity. In stickleback and many other species, it is well known that individuals prefer to associate with familiar individuals over non-familiar ones and that there may be benefits in doing so (Atton et al., 2014; Barber and Ruxton, 2000; Hart et al., 2014; Ward and Hart, 2003). In juvenile grayling (*Thymallus thymallus*), Hart and colleagues (2014) found, for example, that fish paired with a familiar partner were more likely and faster to enter and forage in a novel environment than fish paired with an unfamiliar conspecific. In our experiment, by a mechanism of self-referent matching (e.g., based on odour cues or morphology), fish might have recognised members of their own type (Olsén et al., 2003; Ward et al., 2004, 2005). As a consequence, majority fish may have found themselves in a more familiar social environment, reducing the fear to leave the first pond. Additionally, we again have to consider the role of familiarity with the experimental setup. In later experimental trials, majority fish had a higher likelihood to be tested repeatedly, increasing their familiarity with the setting, which probably contributed to their faster leaving tendencies.

While social effects (although likely not the ones initially anticipated) might have played a role in the fish's behaviour to leave the first pond, we found no indication that fish adjusted in larger-scale movement behaviours between ponds. Costs and limits of behavioural plasticity can impose constraints on the evolution of plasticity (Auld et al., 2010; DeWitt et al., 1998) and high levels of plasticity in one context can limit plasticity in other contexts (Gibelli et al., 2018; Jablonszky et al., 2022). High levels of behavioural plasticity may thus not be favoured in a species with a dynamic fission-fusion social system, such as described for adult sticklebacks (Croft et al., 2005; Ward et al., 2002), if behavioural adjustment due to e.g., energetic costs of movement is too costly. In a process described as (social) niche choice/picking sticklebacks may instead actively select a social group that matches their own phenotype, rather than repeatedly conforming to any given group (Stamps and Groothuis, 2010).

Fish in our mesocosm, had sufficient time and space to actively choose their interacting partners, thus providing more freedom in selecting a social group than in classical lab settings. Furthermore, individual variation in behaviours within a group (i.e., heterogeneity) can trump the benefits of conformity (Jolles et al., 2020). For example, in Trinidadian guppies (*Poecilia reticulata*), behavioural heterogeneity is found to be advantageous in a foraging context, benefitting both shy and bold individuals when interacting (Dyer et al., 2009), or facilitate social learning (Hasenjager et al., 2020) and thus potentially act as a mechanism to maintain individual differences (Montiglio et al., 2013). Lastly, social interactions might have been strongest at the beginning of the experiment when fish were confined to the same pond, likely exerting stronger social effects on the probability to leave the first pond than on movement between ponds. However, we found this explanation unlikely as fish exited the first pond alone rather than in groups most of the time and fish repeatedly encountered other individuals with whom they could associate over the course of the experiment (Fig. 3.4, A4 & A5).

Our results suggest that residents are more plastic than migrants with regards to movement behaviour. One may speculate that resident sticklebacks may display a more ‘reactive’ coping style while migrants may display a more ‘proactive’ coping style. A reactive coping style is characterised by shyness in novel environments, a high degree of behavioural plasticity, and high social responsiveness, while a proactive coping style is characterised by opposite characteristics (Coppens et al., 2010; Koolhaas et al., 1999). In a previous study on wild sticklebacks from the same populations, we found resident sticklebacks to be bolder than migratory sticklebacks (Ramesh et al., 2022). This thus contrasts expectations from the coping-style literature and previous findings in sticklebacks (Bensky and Bell (2022), but see Bensky et al. (2017)). For migratory fish, spring and autumn migration represent an essential part of their life cycle. Large-scale movement behaviour similar to the one measured here is thus closely associated with the populations’ respective life histories. Due to tight links between such migration-like behaviours and the animal’s physiological state (Kitano et al., 2012), it is plausible that these may override social responsiveness in migrants, leading to more stable expression of such behaviours.

Given previous studies on social modulation of individual behaviour such as foraging behaviour (Dyer et al., 2009), locomotion behaviours (Herbert-Read et al., 2013; Wilson et al., 2019), boldness (Jolles et al., 2014) and dispersal tendencies (Cote et al., 2011) it is surprising that we did not find stronger social effects between migrants and residents. We would thus like to point out

some differences between our study and previous work. The most obvious (and perhaps most important) difference between our study and previous work lies in the temporal and spatial scale of the experimental setup. Our experiment lasted for almost a full day and fish could move for several hundreds of meters across the mesocosm. In contrast, typical experiments are performed in the laboratory and thus in relatively small test tanks and often last for only minutes (but see Cote et al. (2011)). Another difference lies in the ecological conditions that animals experienced during the trials. Our mesocosms are positioned outside and thus subjected to natural light and weather conditions and have flowing water (from a typical stickleback habitat). The water thus contains naturally occurring invertebrates and olfactory cues. Conditions in the lab are, almost by definition, more artificial and standardised, largely removing the animal from its ecology. These differences in scale and ecological conditions create more heterogeneity in the environment and offer alternative social options. While experiments in highly confined spaces do not allow individuals to escape from the social setting, in our mesocosm, the fish can spread out and choose their own social environment, reducing the need to adapt to the social setting. Our study highlights that further investigations into the strength of social effects under ecologically relevant settings are warranted.

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APPENDIX

This appendix contains the following elements:

- Figure A1: Setup for monitoring within-pond movement.
- Figure A2: Effect of group composition on within-pond movements.
- Table A1: Pairwise comparison of the probability of exiting the first pond, and number of pond transitions in relation to group composition.
- Table A2: Pairwise comparison of the probability of exiting the first pond, and number of pond transitions in relation to population origin.
- Table A3: Testing the effect of repeated testing (habituation) on movement behaviours.
- Figure A3: The effect of repeated testing (habituation) on movement behaviours.
- Figure A4: Individual movement trajectories over the full length of two representative experimental runs with a lot of movement
- Figure A5: Individual movement trajectories over the full length of two representative experimental runs with little movement

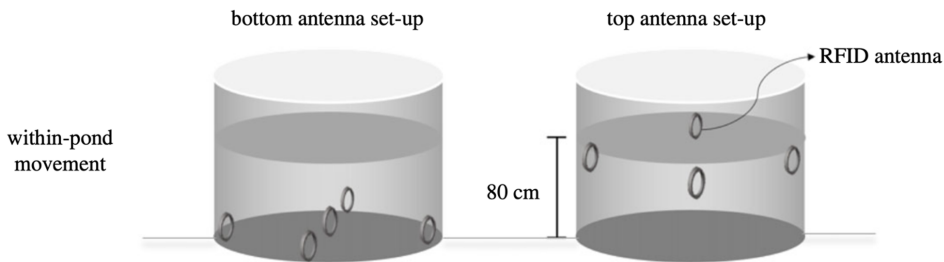


Figure A1 | Setup for monitoring within-pond movement. Connecting tubes were closed off during the first five hours of the experiment so that fish were confined to pond 1. To record movement within the pond, five circular RFID antennas were placed upright on the bottom of the pond, and four antennas were placed upright just below the water surface in a square pattern. All 9 antennas were placed in the first pond of the mesocosm. Figure adapted from Ramesh et al., 2023.

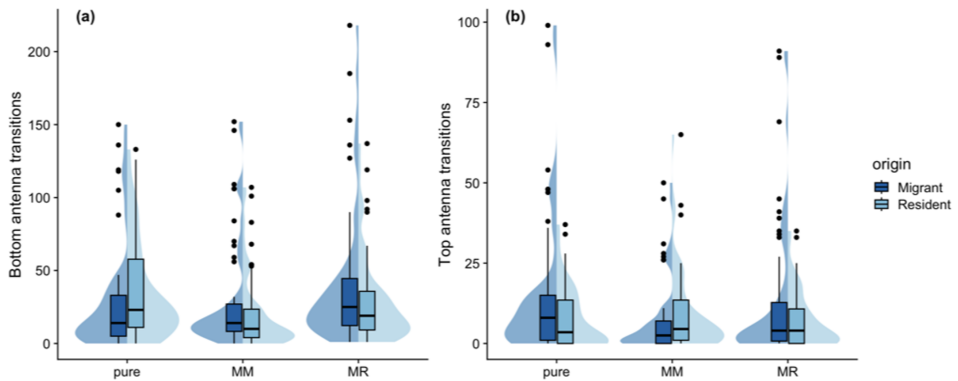


Figure A2 | Effect of group composition on within-pond movements. (a) Number of bottom antenna transitions (‘crosses’) in each of the social groups. (b) Number of top antenna transitions in each of the social groups. The plots indicate that migrants and residents do not differ in within-pond movements and that movement is not affected by the social environment. Pure: group of residents or migrants. MR: group with a majority of residents (7 residents + 3 migrants); MM: group with a majority of migrants (3 residents + 7 migrants). Only individuals’ first test in each experimental group is displayed. Boxes show the median with 25th and 75th percentiles. Whiskers indicate values within 1.5 times the interquartile range, and circles represent values outside this range. Shaded density kernels represent the frequency and distribution of raw data points.

Table A1 | Pairwise comparison of the probability of exiting the first pond, and number of pond transitions in relation to group composition. The estimates of the model for movement tendencies (Probability to exit pond 1 and pond transitions) are given in Table 1. To understand whether the movement tendencies of migrants and residents differed between the different social environments, we performed post-hoc tests using Tukey's pairwise comparison (estimates are represented as log odds ratio for probability to exit pond 1 and represented on log-scale for pond crosses). We can then directly interpret the values of the contrast from the estimate and the 95% C.I. In migrants, the probability to exit pond 1 did not vary when they were tested in different social environments, while residents in mixed groups (MM and MR) are more likely to exit pond 1 than residents in their pure groups. For pond transitions, again migrants did not show variation from their pure groups when presented with different social environments, while residents again moved somewhat more than in their pure groups. This could be also due to habituation effects, see below (Table A3; Figure A3). Estimates with C.I. that do not include 0 are indicated in bold.

	Probability to exit pond 1	Pond transitions
Contrast - migrant	β (95% C.I.)	β (95% C.I.)
pure – MR	0.24 (-5.94, 6.78)	-0.36 (-1.49, 0.73)
pure – MM	-0.42 (-7.50, 6.02)	-0.33 (-1.52, 0.76)
MR – MM	-0.69 (-6.93, 5.21)	0.01 (-0.93, 0.93)
Contrast - resident	β (95% C.I.)	β (95% C.I.)
pure – MR	-5.97 (-15.57, -0.23)	-1.23 (-2.30, -0.15)
pure – MM	-9.05 (-20.68, -2.11)	-1.59 (-2.68, -0.57)
MR – MM	-2.90 (-10.68, 1.85)	-0.36 (-1.25, 0.56)

Table A2 | Pairwise comparison of the probability of exiting the first pond, and number of pond transitions in relation to population origin. Estimates of the model for movement tendencies (Probability to exit pond 1 and pond transitions) are given in Table 1. However, to understand whether the movement tendencies of migrants and residents differed across social environments, we performed post-hoc tests using Tukey's pairwise comparison between migrants and residents (all estimates are represented as log odds ratio for probability to exit pond 1 and represented in log-scale for pond transitions). Contrasts between populations can readily be interpreted from estimate and the 95% C.I. The greatest contrast in movement tendencies between migrants and residents was observed when fish were tested in their respective pure groups. For the probability to exit pond 1, migrants and residents did not differ in mixed groups, as residents increased in probability to exit the first pond, up to a level similar to that of migrants (who did not change in probability to exit pond 1), as shown in Fig 2 and Table 1. Regarding pond transitions, migrants and residents predominantly maintained movement differences, with migrants moving more than residents. However, the difference is less pronounced in majority migrant groups. This variation could also be potentially due to habituation effects, see below (Table A1; Figure A3). Estimates with C.I. that do not include 0 are indicated in bold.

Contrasts	Probability to exit pond 1	Pond transitions
	β (95% C.I.)	β (95% C.I.)
pure: migrant – resident	7.77 (0.69, 20.12)	2.09 (0.70, 3.51)
MM: migrant – resident	-0.84 (-8.19, 5.56)	0.85 (-0.12, 1.87)
MR: migrant – resident	1.39 (-4.52, 7.96)	1.22 (0.28, 2.17)

Table A3 | Testing the effect of repeated testing (habituation) on movement behaviours. Bayesian univariate response models for the probability to exit pond 1 and transitions between-ponds with model specifications as given in the main text. An additional fixed factor of test-order \times origin (to test for differential responses of migrants and residents to the repeated exposure) was fitted. Estimates of fixed effects (β) and standard deviation of random effects are given with their 95% Bayesian credible intervals (C.I.). The model indicates that in residents, yet not in migrants, repeated testing (test order) led to an increase in probability to exit the first pond. Regarding pond transitions, we again observe an effect of test order, such that residents moved more over repeated tests, while the effect is largely absent for migrants.

Fixed effects	Probability to exit pond 1	Pond transitions
	β (95% C.I.)	β (95% C.I.)
intercept (migrant)	5.12 (0.45, 13.17)	1.83 (0.63, 3.04)
origin (resident)	-11.73 (-27.39, -3.74)	-2.79 (-4.43, -1.20)
test order (migrant)	-0.05 (-2.25, 2.16)	0.15 (-0.32, 0.63)
test order (resident)	4.99 (1.54, 11.90)	0.73 (0.12, 0.37)
Random effects	SD (95% C.I.)	SD (95% C.I.)
obs	4.25 (0.56, 10.18)	1.35 (1.15, 1.58)
individual ID	5.90 (2.32, 12.85)	1.79 (0.19, 1.44)
group ID	1.73 (0.11, 4.40)	0.76 (0.45, 1.13)

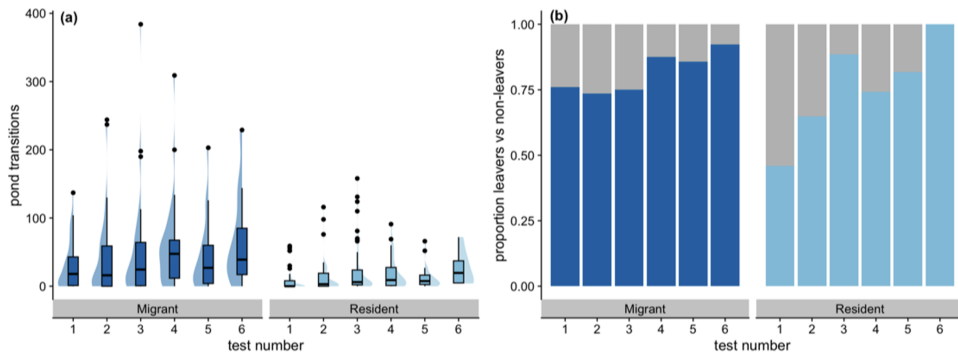


Figure A3 | The effect of repeated testing (habituation) on movement behaviours. (a) Number of between-ponds transitions and (b) proportion of individuals leaving (dark blue for migrants; light blue for residents) versus not leaving (grey) the first pond within 1 h in relation to the experience each fish had with the experimental set-up. As explained in the Methods, individuals were tested repeatedly (some up to seven times) in their majority group. The figure (and the corresponding statistics in Table A1) show that the residents (and, to a lesser extent, also the migrants) tended to move more between ponds with increasing test number (a), and that the tendency to leave the first pond increased markedly with test number in residents and to a smaller extent in migrants (b). Boxes in (a) show the median with 25th and 75th percentiles. Whiskers indicate values within 1.5 times the interquartile range, and circles represent values outside of this range. Shaded density kernels represent the frequency and distribution of raw data points. In (a) and in (b), only test numbers 1 - 6 are shown because only a few individuals were tested seven times.

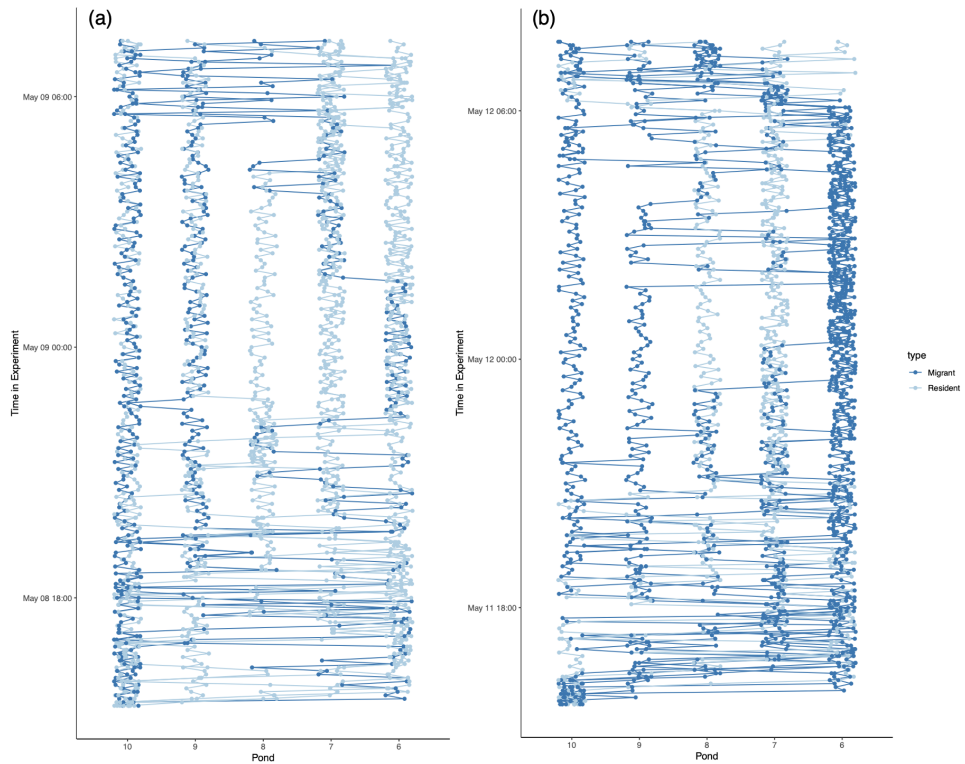


Figure A4 | Individual movement trajectories over the full length of two representative experimental runs with a lot of movement (a) in a majority resident group and (b) in a majority migrant group. Each individual's position in the mesocosm was inferred from PIT tag data every 5 min. In both panels the starting pond is to the left (labelled '10'). Time runs from bottom to top. Figures displaying all experimental runs are available under <https://doi.org/10.34894/6MA5UB>.

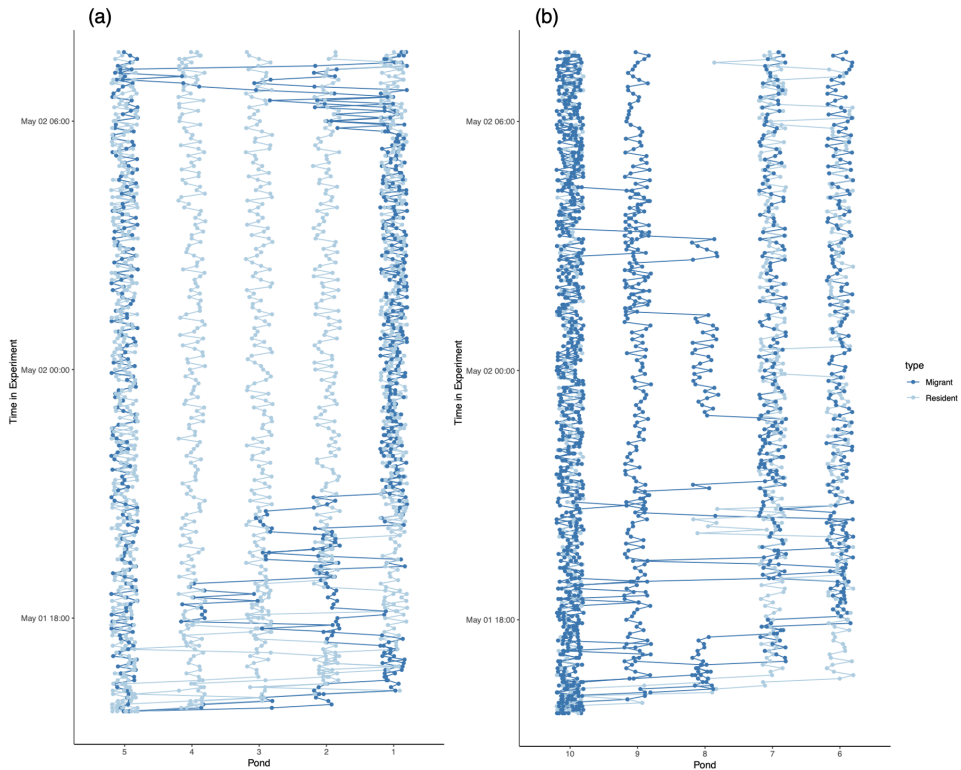


Figure A5 | Individual movement trajectories over the full length of two representative experimental runs with little movement. (a) in a majority resident group and **(b)** in a majority migrant group. Each individual's position in the mesocosm was inferred from PIT tag data every 5 min. In both panels the starting pond is to the left (labelled '5' in (a) and '10' in (b), respectively). Time runs from bottom to top. Figures displaying all experimental runs are available under <https://doi.org/10.34894/6MA5UB>.

