

Social Feedback and the Emergence of Leaders and Followers

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Summary

In many animal groups, certain individuals consistently appear at the forefront of coordinated movements [1–4]. How such leaders emerge is poorly understood [5, 6]. Here, we show that in pairs of sticklebacks, *Gasterosteus aculeatus*, leadership arises from individual differences in the way that fish respond to their partner's movements. Having first established that individuals differed in their propensity to leave cover in order to look for food, we randomly paired fish of varying boldness, and we used a Markov Chain model to infer the individual rules underlying their joint behavior. Both fish in a pair responded to each other's movements—each was more likely to leave cover if the other was already out and to return if the other had already returned. However, we found that bolder individuals displayed greater initiative and were less responsive to their partners, whereas shyer individuals displayed less initiative but followed their partners more faithfully; they also, as followers, elicited greater leadership tendencies in their bold partners. We conclude that leadership in this case is reinforced by positive social feedback.

Results and Discussion

In many animal groups, certain individuals are consistently observed at the forefront of collective movements, and these individuals have thus been described as “leaders” [1–3]. Various studies have identified correlates of leadership, including both physical factors, such as size or physiological state [7–9], and temperamental or personality characteristics, such as activity [1] or boldness [10–13]. However, the social interactions through which leaders attain their status are not well understood [5, 6]. Studies of self-organization have explored how groups of individuals following simple rules can show coordinated behavior but have focused primarily on homogenous associations [5, 14–18]. Here, by contrast, we explore how leadership emerges in pairs of sticklebacks by examining individual differences in the way in which fish respond to each other's behavior.

We investigated how individuals in a pair respond to one another's movements by setting up a simple scenario in which fish were forced to leave cover occasionally in order to look for food in a “risky” environment. Twenty pairs of fish (all of similar sizes) were each placed in a separate tank that had a “safe” resting area (deep water with some weeds) at one end and

a “risky” area (shallow with no shelter) at the other, in which to look for food. For the first four days, an opaque partition prevented fish in the same tank from seeing each other. Each fish was placed in the tank for one hour per day, and a bloodworm (Chironomid larva) was provided every 30 min in the exposed area in order to train the fish to expect food there. After this “training” period, we ran two 1 hr assessments (without delivery of food) during which we recorded the timing of all transitions out of and back into cover (a fish was defined as under cover if partially or wholly obscured by weed when viewed from directly above). On average, individuals made 32.4 ± 4.3 (mean \pm SE) trips out of cover during each 1 hr assessment, which led to their being exposed for $27.8 \pm 3.5\%$ of the time. We counted each time a fish left cover as one trip.

For each individual, we fitted a continuous-time Markov Chain Monte Carlo (MCMC) model [19] in which a fish could be in one of two states: safe (under cover) or exposed. We estimated for each individual fish the tendencies (technically, the transition intensities) to leave cover and to return to cover. Fish temperament [12, 13, 20] was then defined as the ratio between the two transition intensities, such that large values of our temperament score would imply a relatively stronger tendency to leave cover and small values a relatively stronger tendency to return to cover. After a final day of training during which food was again provided for reinforcement of the expectation that food might be found in the exposed, risky area, we randomly paired fish and used our temperament score to define a “bold” fish (relatively stronger tendency to leave cover) and a “shy” fish (relatively stronger tendency to return to cover) within each of the 20 pairs [10, 20–24]. We ran the main experiment over the next four days, during which time no food was delivered in the tank. On two of the days (either the 1st and 3rd or the 2nd and 4th), we recorded the movement of each pair when separated by an opaque partition as in the experiments above (control), whereas on the two remaining days we used a transparent partition that allowed the fish to see each other and thus to potentially interact. When the fish could not see each other, the bolder fish in each pair made 48.1 ± 6.6 trips out of cover, spending $41.3 \pm 5.4\%$ of time exposed, whereas the shyer member of the pair made 17.3 ± 2.4 trips and spent $14.3 \pm 3.5\%$ of time exposed (no difference from their behavior during the previous week, $p \geq 0.17$ for all paired t tests). When members of a pair were allowed to see each other, both the bolder and the shyer fish significantly increased the number of trips (64.3 ± 5.5 and 43.6 ± 4.7 trips respectively) and the amount of time spent out of cover ($50.8 \pm 4.5\%$ and $33.0 \pm 4.8\%$ of time; $p \leq 0.019$ for all paired t tests comparing the transparent with the opaque runs).

When fish were allowed to see each other, the pair also synchronized their trips out of cover, quantifiable by a measure of synchronization analogous to genetic linkage disequilibrium [17, 25] (sync scores in transparent versus sync scores in opaque: 0.81 ± 0.03 versus -0.15 ± 0.11 ; four measurements from each of 20 pairs; ANOVA blocked by fish pair: $F_{1,59} = 183.2$, $p < 0.001$). These synchronized movements were led mostly by the bold fish, which initiated 20.2 ± 2.1 joint trips (averaging across both transparent runs for all pairs), versus

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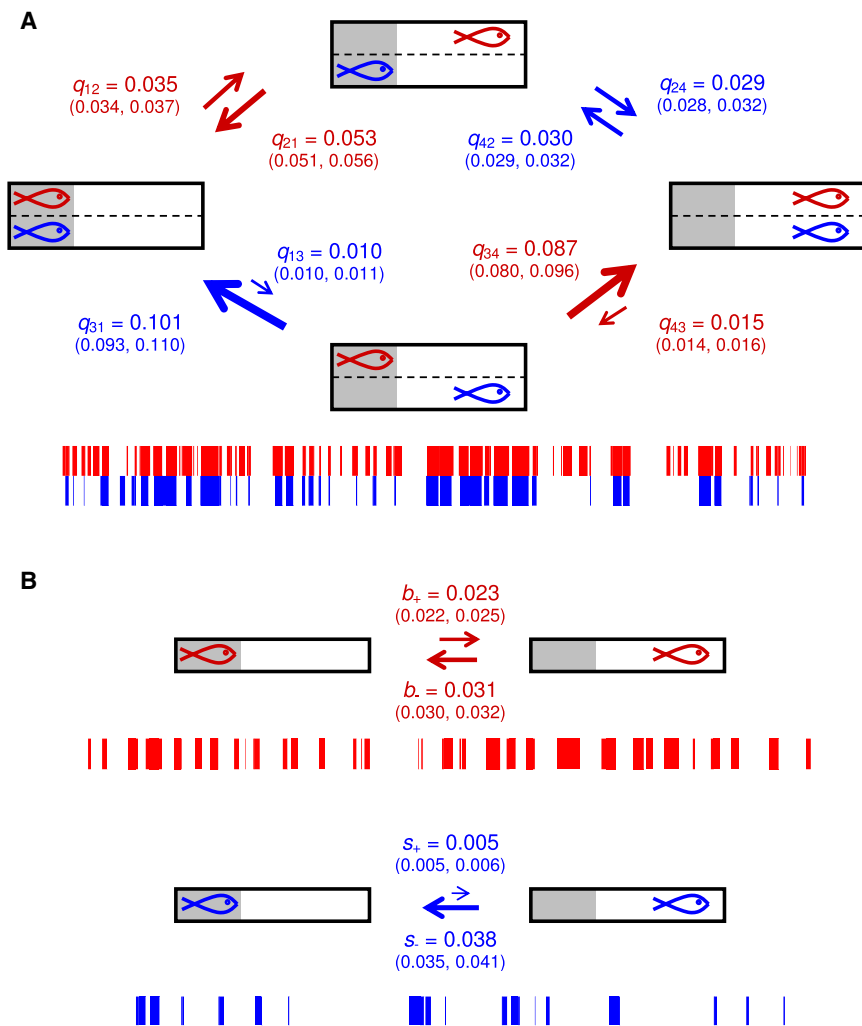


Figure 1. Transition Intensities from the MCMC Model

Transition intensities (best estimate and 95% CI) for leaving and returning to cover, for runs during the main experiment with (A) transparent and (B) opaque partitions. The area in which fish were covered by weed is shown in gray, the exposed area in white. The bold fish and associated transitions and intensities are shown in red, the shy fish and associated transitions and intensities in blue. Length and thickness of arrows is scaled according to transition intensity. Note that during opaque runs, a simplified model in which fish did not respond to one another's movements (B) gave the best fit; the transition intensities for this model are denoted b_+ and b_- for the bold fish and s_+ and s_- for the shy fish. The area of each arrow is proportional to the magnitude of the relevant transition intensity. Below each diagram of transitions, we show an illustrative set of results from one pair: time runs from left to right, periods during which the bold fish was out of cover are indicated by red shading, and periods when the shy fish was out are in blue. For the transparent treatment illustrated in (A), results for both fish are juxtaposed to highlight synchrony.

only 10.0 ± 1.4 joint trips initiated by the shy fish. We counted one joint trip whenever, beginning with both fish under cover, one fish (the leader) left cover and, before returning, was joined by the other (the follower). To determine how the bold individual emerged as leader, we used a continuous-time MCMC model with four possible, numbered states (Figure 1A): 1, both fish safe (under cover); 2, bold fish exposed, shy fish safe; 3, bold fish safe, shy fish exposed; and 4, both fish exposed. The transition intensities from this model provide us with a precise description of the behavior of both the bold and the shy fish and the way in which they respond to one another's movements (q_{ij} denotes the transition intensity from state i to state j). The tendency to leave cover when the partner is still concealed (q_{12} for the bold fish or q_{13} for the shy fish) gives us an individual's "initiative," which may differ from its tendency to join a trip out of cover initiated by the other individual ("gregariousness"; q_{34} for bold or q_{24} for shy). Similarly, the tendency of a fish to remain out of cover by itself while the other individual is concealed (its "determination"; the inverse of q_{21} for bold or of q_{31} for shy) differs from its tendency to remain out of cover during a joint trip (its "faithfulness"; the inverse of q_{43} for bold or of q_{42} for shy). Figure 1A illustrates this model fitted to the transparent runs, during which the fish could see each other.

Inspection of the transition intensities in Figure 1A reveals that the bold fish in a pair was more likely to leave cover

than was the shy fish, both on its own (when its partner was under cover) and in company (when its partner was already out of cover). We can also see that the fish responded to each other, as we expected from the synchronization scores discussed earlier: both fish were more likely to leave cover if their partner was already out ($q_{34} > q_{12}$, $p < 0.001$; $q_{24} > q_{13}$, $p < 0.001$) and were less likely to return to cover under the same circumstances ($q_{43} < q_{21}$, $p < 0.001$; $q_{42} < q_{31}$, $p < 0.001$; Figure 1A). Constraining the model so that the possibility of such responses was ignored (i.e., requiring that the tendencies to leave or to return to cover should be identical regardless of whether the partner is under cover or not, so that $q_{12} = q_{34}$, $q_{13} = q_{24}$, $q_{21} = q_{43}$, and $q_{31} = q_{42}$) leads to a significant decrease in fit ($\chi^2_4 = 2327.8$, $p < 0.001$). Reassuringly, if we fit the same model to the runs with an opaque partition, during which the fish could not see each other, we obtain the opposite result, with the simpler model in which fish cannot respond to one another's movements (Figure 1B) giving the best fit (allowing for such responses leads to no increase in the explanatory power of the model: $\chi^2_4 < 0.1$, $p = 0.99$). Transition intensities estimated from the opaque runs were also highly correlated with estimates from individual runs in the previous week ($r_{38} = 0.61$, $p < 0.001$).

Comparing the transition intensities estimated from the opaque runs and the intensities from the transparent runs allows us investigate the degree to which the two fish differ in their responses to one another. In opaque runs, for the bold fish, we write b_+ for the transition intensity out of cover and b_- for the transition intensity back into cover; equivalent intensities for the shy fish are denoted s_+ and s_- . Although both fish increased their tendency to leave cover (both initiating and joining) when they could see one another compared to when they were in isolation, the proportional increase for the shy

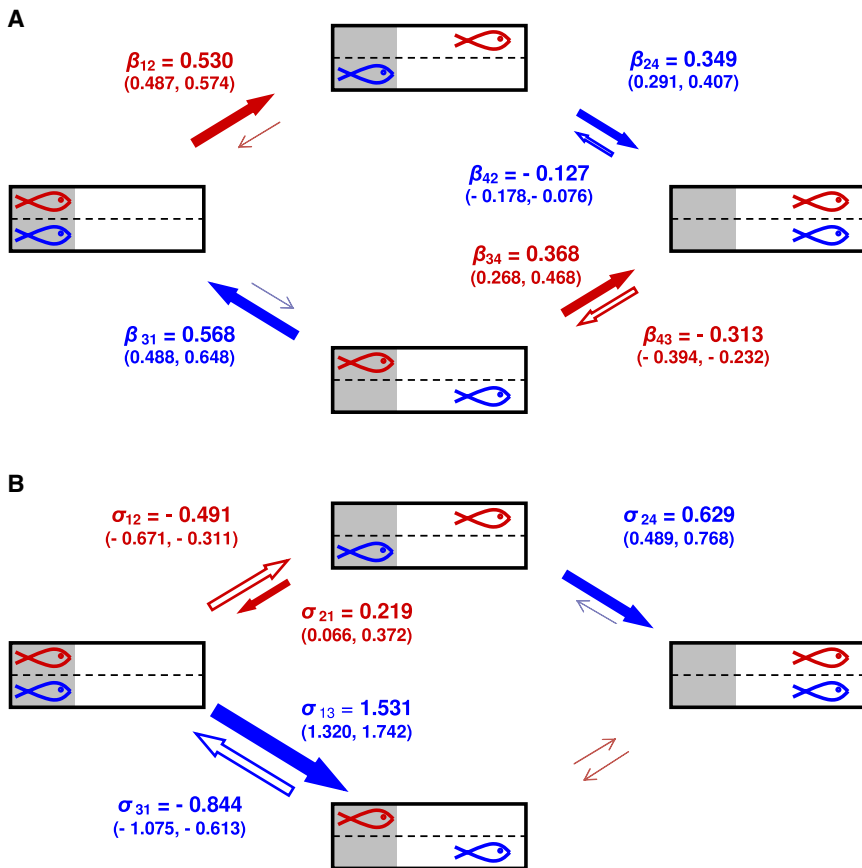


Figure 2. Effect of Individual's Temperament on Transition Intensities

Log-linear effects (best estimate and 95% CI) of (A) bold and (B) shy fish-temperament scores on the transition intensities (β_{ij} denotes effect of bold fish temperament on q_{ij} ; σ_{ij} denotes effect of shy fish temperament on q_{ij}). The bold fish and associated transitions and effects are shown in red, the shy fish and associated transitions and effects are shown in blue. Thick solid arrows represent significant positive effects on a transition, thick empty arrows represent significant negative effects, and slim arrows (without coefficients) represent nonsignificant effects. The area of each arrow is proportional to the magnitude of the relevant effect.

fish was significantly greater than that for the bold fish (initiating: $q_{13} / s_+ = 1.82 \pm 0.11$ for shy, versus $q_{12} / b_+ = 1.51 \pm 0.05$ for bold, $p = 0.007$; joining: $q_{24} / s_+ = 5.52 \pm 0.27$ for shy, versus $q_{34} / b_+ = 3.73 \pm 0.19$ for bold, $p < 0.001$). Compared with isolated individuals, fish that could see their partner were also more likely to return to cover if exposed alone, and the proportional increase was once again greater for the shy fish ($q_{31} / s_- = 2.69 \pm 0.15$ for shy, versus $q_{21} / b_- = 1.72 \pm 0.06$ for bold, $p < 0.001$). When exposed in company, however, fish that could see their partner were less likely to return to cover than were isolated individuals, and the proportional decrease was greater for the bold fish ($q_{42} / s_- = 0.81 \pm 0.04$ for shy, versus $q_{43} / b_- = 0.48 \pm 0.02$ for bold, $p < 0.001$).

The above results show that bold and shy fish differ in their social behavior. If the crude, dichotomous definition of "shy" and "bold" is so informative, it is reasonable to ask whether a more refined definition of temperament would do better. We tackled this question by fitting our measures of individual temperament (the ratio of leaving cover intensity versus returning to cover intensity that was estimated for each fish in isolation with the opaque partition) as covariates in the MCMC model describing movement of the pair with the transparent partition. Including the individual temperament scores of both fish led to a significant increase in model fit ($\chi^2_{16} = 1302.1$, $p < 0.001$; Figures 2A and 2B), and it was superior to considering the detailed temperament of only one of the two fish (bold fish temperament: $\chi^2_8 = 425.7$, $p < 0.001$; shy fish temperament: $\chi^2_8 = 834.4$, $p < 0.001$). For both the bold and the shy individual, fish with a stronger propensity to leave cover in isolation with the opaque partition (large temperament score) showed a similar behavior when in a pair, as denoted by

significant positive effects of an individual's temperament score on the transition intensities associated with that individual leaving cover by itself (95% CI: $0.487 < \beta_{12} < 0.574$ for bold; 95% CI: $1.320 < \sigma_{13} < 1.742$ for shy; Figures 2A and 2B), and, for the shy fish, a significant negative effect on its tendency to return to cover when exposed alone (95% CI: $-1.075 < \sigma_{31} < -0.613$). Similar effects were seen in the transitions that refer to joint trips, with significant positive effect of a fish's temperament on its tendency to leave cover to join a companion (for bold, 95% CI: $0.268 < \beta_{34} < 0.468$; for shy, 95% CI: $0.489 < \sigma_{24} < 0.768$) and, for the bold fish, a significant negative effect on its tendency to terminate that joint trip (95% CI: $-0.394 < \beta_{43} < -0.232$).

In addition, an individual's temperament affected not only its own behavior but also that of its partner; constraining the MCMC model by fixing at zero the influence of each fish's temperament score on transition intensities corresponding to movement of the other fish led to a significant decrease in fit ($\chi^2_8 = 331.8$, $p < 0.001$). By contrast, the same constraint leads to no loss of fit when the model is applied to runs with the opaque partition ($\chi^2_8 < 0.1$, $p > 0.9$). A bold fish with a higher temperament score proved a more convincing leader, increasing the tendency of the shy fish to join it out of cover (95% CI: $0.291 < \beta_{24} < 0.407$) and decreasing its tendency to abandon a joint trip (95% CI: $-0.178 < \beta_{42} < -0.076$). The shy fish also became more prone to return to cover when exposed alone if it was paired with a bold fish with a high temperament score (95% CI: $0.488 < \beta_{31} < 0.648$). A shy fish with a relatively lower temperament score had an even more dramatic effect on its partner, as the bold fish became more prone to leave cover on its own (95% CI: $-0.671 < \sigma_{12} < -0.311$) and less likely to return to cover if exposed alone (95% CI: $0.066 < \sigma_{21} < 0.372$). Thus, very bold individuals made better leaders, enhancing the followership characteristics of their shy partners. At the same time, very shy individuals made better followers and elicited greater leadership tendencies in their bold partners.

In summary, our results show that leadership can emerge from temperamental differences between members of a pair, which influence the way in which individuals respond to one another. Bolder individuals emerged as leaders not only

because of their greater tendency to leave cover (which was apparent both in a pair and in isolation) but also because they were less responsive to the movements of their partners. By contrast, it was the shy individuals, which were more strongly influenced by their partners' behavior, that emerged as followers. It is also clear, however, that these pre-existing temperamental differences are reinforced by social feedback—a bold, unresponsive individual induced greater followership characteristics in its partner, whereas a shy, responsive individual had the opposite effect, inducing leadership characteristics.

Models of self-organization have had great success in explaining how complex group movements can arise from the interaction of individuals following simple rules [5, 14–16, 18], particularly in large, homogeneous associations of social insects [16, 26–29]. Our results imply that the power of this approach, as well as its applicability to vertebrates [14], may be still further enhanced by taking into account variation among individual group members in the rules that they follow, particularly the ways in which they respond to one another [6]. When individuals are capable of perceiving and responding to the individual temperaments of their social partners (as is the case in our study), the behavior of a group is likely to reflect its composition in terms of individual “personalities.” Paradoxically, a deeper understanding of collective action may thus depend upon the study of differences in the behavior of individuals.

Experimental Procedures

Study Organism and Equipment

A stock of three-spined sticklebacks, *Gasterosteus aculeatus*, was collected from the Swaffham Bulbeck area of the River Cam (UK) during 2006 and kept in a lab at $17^{\circ}\text{C} \pm 1^{\circ}\text{C}$ on a 10L:14D light regime for at least one month before being used in experiments. All fish were taken from the same population, because variation in personality may be influenced by evolutionary history [21].

Fish were kept in large glass aquaria with dual filtration systems (under-gravel and external Hagen filters). Tanks were lined with gravel and contained a number of plastic plants (Hagen). The sex of individual sticklebacks was not established, but the standard laboratory temperature used prevented them from coming into breeding condition [30]. Fish used in experiments were of similar length ($45 \text{ mm} \pm 5 \text{ mm}$ from tip of snout to peduncle), for removal of size as a potentially confounding variable [31]. All sticklebacks were fed to satiation daily on frozen bloodworms (Chironomid larvae). All experiments were approved by the Animal Users Management Committee of the University of Cambridge.

Experimental Setup

Fish to be trained for experiments were moved to partitioned holding tanks ($60 \text{ cm} \times 30 \text{ cm} \times 40 \text{ cm}$). Each glass tank held six fish in individual compartments, which were separated by transparent plastic partitions. This allowed individual fish identification but minimized any stress caused by isolation. Under-gravel filtration operated over the whole system, and each compartment had a plastic plant at one end and a white plastic tile (approximately 1.5 cm^2), onto which food was delivered, at the other.

During training and observation, fish were transferred to glass experimental tanks ($90 \text{ cm} \times 30 \text{ cm} \times 30 \text{ cm}$; see Figure S1, available online). The walls of these tanks were covered with black opaque plastic, preventing external movement from being seen by the fish. Each tank was partitioned lengthwise with either an opaque or a transparent plastic barrier, forming two long compartments. The tanks were lined with white gravel in such a way that a slope was created from a deep end, with a water depth of 12 cm, to a shallow feeding end, with a water depth of 2 cm. Two plastic plants (Hagen) were placed in the deep end of each compartment, and a feeding tile similar to those used in the holding tanks was placed at the other end. A small, vertical, white plastic screen ($8 \text{ cm} \times 8 \text{ cm}$, visible above the gravel) was put in front of each feeding tile, preventing fish at the shallow end of the tank from seeing food at the deep end. Water was aerated when

fish were not present in the tank. After the fish were allowed five minutes for acclimation to the new environment, their behavior was recorded with a Sony DCR-35E digital video camera, mounted directly above each tank, aligned to give a full view of the whole tank.

Training and Assessment of Individual Temperament

Data were collected in fortnightly cycles, with fish spending one hour each weekday in the experimental tanks for either training or experimental purposes. The first three days of a cycle were used for training purposes and carried out with the use of the opaque partition for the prevention of visual contact between individuals. Before any hour-long session, a single medium-sized bloodworm was placed onto the feeding tile in each tank. Fish were then individually moved from the holding tanks to the deep end of an experimental tank. After 30 min, tanks were inspected, and a second bloodworm was placed on the tile if the first had been consumed. Any fish that failed to consume two bloodworms on any given day were fed in the holding tanks after training, ensuring that all fish received the same quantity of food during the cycle.

After three days, fish that had failed to eat any bloodworms during training were excluded from the experiment, and the rest then underwent “individual temperament” assessments. This was done through video recordings of the fish in the experimental tanks (with opaque barriers) for an hour on each of the two following days. No bloodworms were provided in the tanks during this assessment (as feeding could influence foraging tendencies); fish were fed a single bloodworm each upon being returned to the holding tanks. See below for details of how temperament was scored. Over the weekend, sticklebacks were not trained but were left in their individual holding tanks and fed daily with one bloodworm.

Interaction among Pairs of Individuals

Assessed fish were assigned to pairs. All of these fish individually underwent an additional day of training at the start of the second week, after having not been exposed to food in the experimental tanks over the four previous days. The final four days of the experimental cycle were used for testing the response to a foraging partner. Each pair was observed twice with an opaque partition and twice with a transparent partition. No food was given each day until the tests had been completed.

Data Analysis

Videos were played back at four times the normal speed, and we recorded the timing of all transitions into and out of cover using a custom-designed data logger. To assess temperament when fish were in isolation, we fitted a continuous-time MCMC model [19], in which a fish could be in two states (under cover, i.e., partially or wholly obscured by weed when viewed from above; or exposed). The model was fitted with the package *msm* v0.8 (written by Christopher Jackson) in R 2.7.0 (R Core Development Team). Temperament was measured as the relative tendency to leave rather than to return to cover; i.e., the ratio of the transition intensity for leaving cover to the transition intensity for returning to cover. Previous work has shown that individual sticklebacks show consistent responses to predation risk [10, 21]. Temperament scores obtained for the same fish during the initial assessments were highly correlated with estimates obtained a week later during the main experiment when the opaque partition was in place ($r_{38} = 0.61$, $p < 0.001$).

We investigated the interaction of pairs of individuals by fitting a continuous-time MCMC model with four possible states: both fish under cover, one fish exposed and one under cover (two possible states), and both fish exposed. The fish with a higher temperament score within the pair was termed “bold,” and the fish with a lower score “shy” (Figure S2). To test whether a fish's behavior was affected by its partner, we also fitted models in which selected transition intensities were constrained to be equal and compared the fit of these reduced models against that of the more general model. The comparison was conducted with a log-likelihood ratio test, which follows a χ^2 distribution, with degrees of freedom equal to the difference in the number of parameters between the two models. We also expanded the (unconstrained) model to include the fish-temperament scores during the trials with an opaque partition as covariates. In this way, we were able to determine whether temperament (measured during the experiments with an opaque partition) influenced transition probabilities (during the experiments with a transparent partition).

Supplemental Data

Supplemental Data include two figures and can be found with this paper online at [http://www.current-biology.com/supplemental/S0960-9822\(09\)00554-5](http://www.current-biology.com/supplemental/S0960-9822(09)00554-5).

Acknowledgments

We acknowledge R. Bergmueller, C. Hinde, and N. von Engelhardt and two anonymous referees for helpful comments on the manuscript. The work was funded by a grant from the Association for the Study of Animal Behaviour to A.M., a NERC studentship to J.H., and a Nuffield Science Bursary to T.Z.A. We thank I. Goldstone for looking after the fish and building the equipment used in these experiments.

Received: November 2, 2008

Revised: December 17, 2008

Accepted: December 22, 2008

Published online: January 29, 2009

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