In a recent paper, we showed that leadership arises from individual behavioral differences in pairs of foraging stickleback (*Gasterosteus aculeatus*). Foraging data from randomly combined pairs of fish were analyzed using Markov Chain models to infer the individual movement rules underlying joint behavior. While both fish responded to partner movement, bolder individuals were the least responsive and showed greater individual initiative. Shy partners were more faithful followers and were also found to bring about greater leadership tendencies in their bold partners. The ability of such followers to inspire bolder fish suggests that leadership may be dependent on individual temperament differences, reinforced by social feedback.

Group living is an essential strategy for many species in the animal kingdom. In order to maintain cohesion, coordination is required, and “leaders” may be seen to emerge at the front of collective movement patterns. Studies have found leadership to correlate with a range of factors including size, activity levels and boldness but have previously not investigated the social interactions that result in leadership status being achieved.

Having established that three-spined stickleback consistently differed in their propensity to leave cover independently, we used a simple scenario in which pairs of fish were forced to look for food in a “risky” environment to investigate how individuals responded to each other. Each individual could be considered in two states, either “safe” (under cover) or “exposed” (no cover). Using a continuous-time Markov Chain Monte Carlo (MCMC) model we estimated the tendency for each fish to leave or return to cover. When paired, fish synchronized their behavior, being more likely to go out if the other was out and return if the other already had done so. Our method allowed us to explicitly quantify the behavioral responses to the different foraging states as illustrated in Figure 1. We were able to consider the role that individual boldness differences have in driving pair-wise foraging interactions using temperament scores reflecting the propensity for fish to leave and return to cover when in isolation. Bold individuals showed greater initiative when paired and shy fish were the most likely to return to cover if their partner had, illustrating that bold and shy fish differed in their social tendencies. Most interestingly, we also discovered that an individual’s leadership and followership potential was influenced by the behavior of its partner; the most outgoing individuals enhanced shy fish joining tendencies while very shy individuals elicited greater leadership tendencies in their more outgoing partner.

This experiment uses a novel method to give us a descriptive insight into the conditions necessary for producing leaders in groups. While MCMC models have been used previously to investigate behavioral phenomena, they enable us here to determine, for the first time, the specific mechanisms responsible for the emergence of leadership. Bold fish were most commonly found to become leaders, but this was due to their limited responsiveness...
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to shy fish movement and to the enhanced followership by their partners as well as a naturally greater tendency to leave cover. Contrary to the idea that certain individual consistently appear at the forefront of coordinated movement,\textsuperscript{10} this suggests that leadership may not be fixed and social feedback is an important source of reinforcement.

Models and studies of self-organization have shown that complex patterns of group behavior can emerge from the interaction of individuals following simple rules.\textsuperscript{11,12} Typically, such studies adopt a "bottom-up" approach, in which more or less detailed knowledge of individual behavior is used to construct a realistic set of individual "rules", from which one attempts to predict the group-level patterns to which these rules will give rise.\textsuperscript{13,14,16} By contrast, the simplicity of our system (the interaction of just two individuals in a controlled and simple experimental setting) allows us to take a "top down" approach, in which we start with the observed pattern of pair behavior, and use maximum likelihood methods to infer the parameters of the underlying individual rules that best explain the data.

One of our key findings is that bolder and shyer fish in a pair adopt different rules. In particular, they respond differently to one another’s movements. This difference is reinforced by social feedback, such that shyer individuals encourage greater initiative on the part of their bolder partners, while bolder individuals inspire their companions to follow them more faithfully. Leadership emerges from these differences in individual behavior. Since most models of self-organization have focused on the behavior of homogeneous groups,\textsuperscript{17-19} and have ignored individual differences, our results suggest some new directions for future modeling efforts.\textsuperscript{20} Moreover, the few existing attempts to incorporate individual differences into models of collective behavior have tended to focus on state variables that affect individual expected payoffs—such as differences in individual energetic reserves\textsuperscript{21,22} or information.\textsuperscript{11} Our findings, by contrast, suggest that there may be consistent temperamental differences among individuals in the way in which they respond to one another, differences that do not reflect immediate payoffs. This raises the intriguing question whether such personality variation enhances group coordination and efficiency, and whether selection for effective collective action might thus help to explain the evolution of personality differences in the first place.

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