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Experience overrides personality differences in the tendency to follow but not in the tendency to lead

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In many animal groups, coordinated activity is facilitated by the emergence of leaders and followers. Although the identity of leaders is to some extent predictable, most groups experience frequent changes of leadership. How do group members cope with such changes in their social role? Here, we compared the foraging behaviour of pairs of stickleback fish after a period of either (i) *role reinforcement*, which involved rewarding the shyer follower for following, and the bolder leader for leading, or (ii) *role reversal*, which involved rewarding the shyer follower for leading, and the bolder leader for following. We found that, irrespective of an individual's temperament, its tendency to follow is malleable, whereas the tendency to initiate collective movement is much more resistant to change. As a consequence of this lack of flexibility in initiative, greater temperamental differences within a pair led to improved performance when typical roles were reinforced, but to impaired performance when typical roles were reversed.

1. Introduction

In many animal groups, coordinated activity is facilitated by the emergence of a leader who initiates and/or directs group movement, with other members of the group adopting the role of follower [1–3]. Studies have shown that leaders may have greater need to impose their preferences on the rest of the group [4–11], they may possess superior information about the best choice of action [1,12–14], or they may simply be temperamentally less willing to follow others [3,15]. Nevertheless, although leadership is to some extent predictable, most groups experience frequent changes of leader, either intermittently [16–19], or as part of a regular pattern of alternation ('turn taking') [20,21]. How do group members cope with such changes in their social role?

The ability of individuals to respond to change in leadership might depend on personality. Theoretical modelling predicts that differences in responsiveness can be a driving force for the emergence and maintenance of personality differences in animals, with less responsive individuals becoming leaders and more responsive individuals becoming followers [3]. Furthermore, personality differences and responsiveness can coevolve through a positive feedback [22]. In support of these ideas, many empirical studies have shown that shyer individuals are more responsive to others, whereas bolder individuals are less responsive [15,23–25]. Consequently, one might predict that bolder individuals should perform poorly when forced to adopt the role of follower, whereas shy individuals should adapt more easily to the role of leader. To the best of our knowledge, however, the ability of bold and shy individuals to cope with different social roles has never been tested.

Here, we test experimentally how well individual stickleback fish in a foraging pair can adapt to changes in leadership. In particular, we seek to compare the behavioural adaptability of bold and shy fish to the roles of leader and follower. Our previous work has shown that this species displays consistent individual differences in the tendency to emerge from cover (i.e. variation in
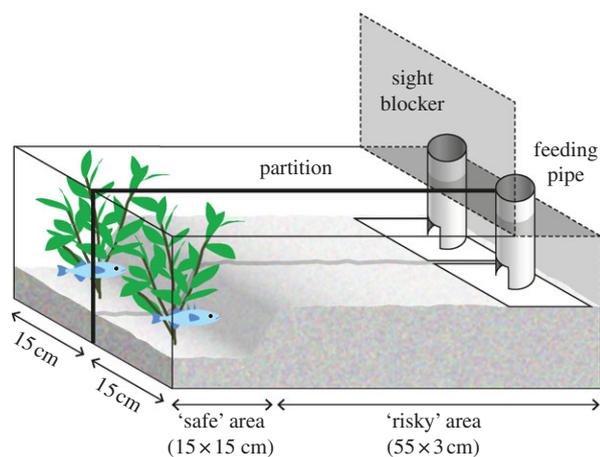
Figure 1. Schematic view of the experimental tank. A sight blocker (area with dashed border line) is made of opaque cardboard to prevent fish in the tank from seeing the human experimenter.

personality [26]), and that when foraging pairs synchronize their emergence from cover, the bolder pair member typically leads [11,15,25]. In this study, we manipulated social roles within a number of pairs through either (i) *role reinforcement*, which involved rewarding the shyer follower for following, and the bolder leader for leading, or (ii) *role reversal*, which involved rewarding the shyer follower for leading, and the bolder leader for following (a schematic view of the experimental set-up is shown in figure 1). We then used continuous-time Markov models to quantify the tendency of bolder and shyer members of both role-reinforced and role-reversed pairs to initiate collective movement and to follow their partners. In this way, we could assess the ability of both bolder and shyer individuals to adapt to changes in leadership.

2. Material and methods

(a) Study animals

Three-spined sticklebacks were collected with a sweep net from a tributary of the River Cam (outskirts of Cambridge, UK) during 2010. Fish were immediately transferred to our laboratory at the University of Cambridge, and housed in two large glass tanks ($120 \times 60 \times 60$ cm), each containing about 100 fish. Fish were allowed to habituate to laboratory conditions for at least one month before being used for any experiment. Each holding tank was equipped with artificial plants, aeration and an under-gravel filtering system. Fish were fed to satiation daily on frozen bloodworms (chironomid larvae). Temperature was set at $12 \pm 1^{\circ}$C, with a controlled photoperiod of 10 L : 14 D cycles, which prevented fish from becoming sexually active [27].

(b) Temperament assessment

Fish to be used in experiments were moved to partitioned holding tanks ($60 \times 30 \times 40$ cm) for individual identification. Each fish was individually held in one of six compartments ($10 \times 30 \times 40$ cm each), separated by transparent partitions that allowed fish to see their neighbours and minimize stress. Each compartment was lined with gravel, with one artificial plant for a shelter and one white plastic plate (2×2 cm) on which food was delivered. Each fish received two medium-sized bloodworms daily. Water quality was maintained through an undergravel filtration system.

Fish were allowed to acclimate for two days in the compartments, and then individual temperament was assessed using the same set-up adopted in our previous experiments [11,15, 21,25,28,29]. An experimental tank ($70 \times 30 \times 30$ cm) was divided lengthwise into two long lanes with an opaque plastic partition (figure 1). Each lane was lined with gravel to create a 'safe', deep, covered area (15 cm depth) with an artificial plant at one end, and a 'risky', shallow, exposed area (3 cm depth) at the other. A white plastic plate (10×15 cm) and a grey PVC feeding pipe (approx. 5 cm) with an opening (3×3 cm) facing the 'safe' end were present at the 'risky' end of each lane to make the set-up identical to the one used in later experiments. The feeding pipe was placed in such a way that its opening was facing slightly outward to prevent the fish in the next lane from seeing inside the pipe. A cardboard barrier was placed on top of the aquarium, in front of the feeding pipes, to prevent fish from seeing the human experimenter. During each temperament assessment, an individual fish was placed at the 'safe' end of a lane, and after 10 min acclimation, its behaviour was recorded from above for 2 h using a video camera (Toshiba Camileo X100, Toshiba Corporation, Japan). When the recording was finished, fish were transferred back to their individual compartments and fed on two medium-sized bloodworms daily.

From the video playback, the horizontal position of a fish was tracked at five frames per second using automated motion-tracking software (ANTRACKS v. 0.99, http://www.antracks.org). From the tracking, we determined the time fish spent in each area ('safe' versus 'risky'), and estimated individual temperament as the proportion of time spent in the 'risky' area. This measure is known to be highly repeatable in this species [15], and we have used this measure in our previous works [11,15,21,25,28,29].

(c) Experimental procedures

Each fish with a relatively high temperament score (i.e. bold fish, temperament range 0.32–0.51) was randomly paired with a fish with relatively low temperament score (i.e. shy fish, temperament range 0.14–0.27). Bold and shy fish did not significantly differ in body length (46.4 ± 0.64 mm and 47.3 ± 0.36 mm, respectively; $t = -1.29$, d.f. $= 34$, $p = 0.206$). Fish in a pair were randomly designated as either leader or follower, creating eight pairs with a bold leader and a shy follower (referred to as 'role-reinforced' pairs), and 10 pairs with a shy leader and a bold follower ('role-reversed' pairs). The 'role-reinforced' and 'role-reversed' labels stem from the fact that, in three-spine sticklebacks, as well as in many other species, bold individuals are known to emerge naturally as leaders and shy individuals as followers when they move into a risky foraging area [15,25,30].

Pairs were transferred one at a time to the experimental tank, with one individual in each lane. This time, the tank was divided with a transparent partition instead of an opaque one, through which fish could see one another. After a 10 min acclimation period, the experimenter delivered a food item (one very small bloodworm together with approx. 2 ml of water via a pipette) in the feeding pipe on the designated leader's side every time it left cover while its partner was still under cover (regardless of whether it was followed by the partner), and did the same for the designated follower every time it followed the designated leader out of cover. When the behaviour of the pair contradicted their designated social roles (i.e. when the designated follower initiated a trip out of cover or when the designated leader followed it) the experimenter delivered a pipette with approximately 2 ml of water taken from a container full of blood worms (thus providing the same smell cues as a successful trip, but without any actual reward in terms of food).

The experiment was run either until 2 h had elapsed or until the designated leader had consumed 40 food items (roughly equivalent to a daily food portion in wet weight). After each
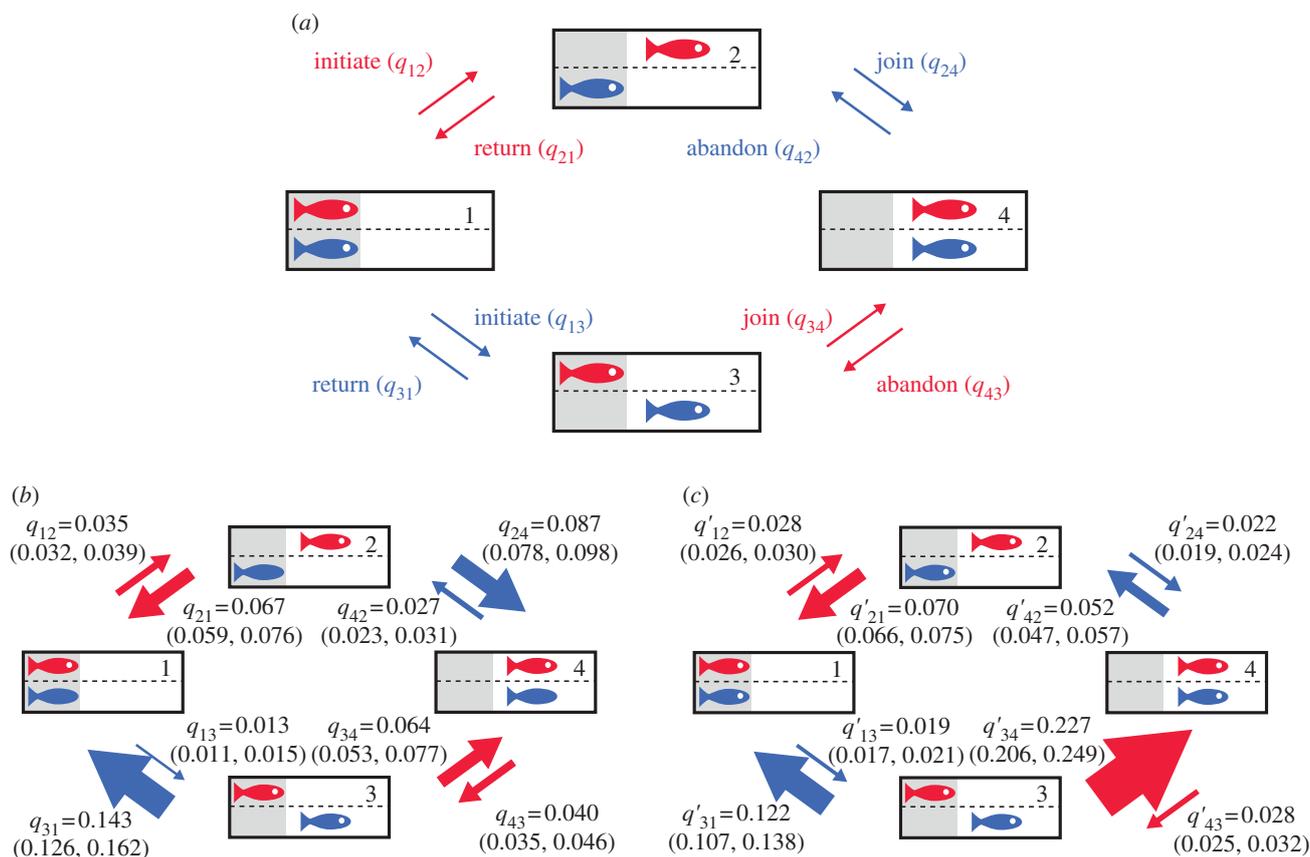
Figure 2. An explanation of a Markov model and the best estimates of transition intensities. (*a*) Each box represents the experimental tank, where fish move between a 'safe' covered area (grey) and a 'risky' exposed area (white). The number in the top-right corner is a state number, and q_{ij} represents a transition intensity from state i to state j. Bold fish and their movements are show in red, and shy fish and their movements are show in blue. Below are the best estimates (and 95% CIs) for (*b*) role-reinforced pairs, and (*c*) role-reversed pairs. Arrow width is scaled to the transition intensity.

experimental session, fish were returned to their individual compartments and fed the appropriate amount of food such that all fish eventually received 40 bloodworms each day. The experiment was repeated for four consecutive days, and fish behaviour was video-recorded as described above.

(d) Data analysis

From the video playback, the position of each fish in the tank was tracked as described for the temperament assessment. To determine the movement rules followed by individuals in each treatment, we applied a continuous-time Markov model to the observed data (figure 2a), in which the position of a pair was categorized as falling into one of four distinct states at any given time: both fish were under cover (state 1); the bold fish was out of cover and the shy fish was under cover (state 2); vice versa (state 3); or both fish were out of cover (state 4). In each pair, on the last day of the experiment, this Markov model was fitted to the time series of state transitions so as to estimate transition intensities between pairs of states. These transition intensities, denoted q_{ij}, for the transition from state i to state j, reflect biologically meaningful decisions in terms of group coordination. Transition intensity q_{12} represents the tendency of the bold fish to leave cover alone (i.e. to initiate a trip), q_{21} the tendency of the bold fish to terminate a trip while out alone, q_{34} the tendency of the bold fish to join a shyer partner that is already out, and q_{43} the tendency to terminate the joint trip; for the shy fish, the same tendencies are represented by the transition intensities q_{13}, q_{31}, q_{24} and q_{42}, respectively. Thus, q_{12} and q_{21} allow us to quantify the tendency of the bold to lead, and q_{34} and q_{43} provide an analogous measure for its tendency to follow (for the shy, the corresponding intensities are q_{13} and q_{31} to lead, and q_{24} and q_{42} to follow).

The simplest null model of movement would be one in which the fish ignore one other, so that $q_{12} = q_{34}$, $q_{21} = q_{43}$, $q_{13} = q_{24}$ and

$q_{31} = q_{42}$ (implying that the tendency of either fish to leave or return to cover is the same, regardless of its partner's location). We have already shown in previous papers [15,25] that this null model can be rejected, and that fish are more likely to join a partner than to initiate a trip by themselves (i.e. $q_{12} < q_{34}$ and $q_{13} < q_{24}$). The impact of changes in social role was investigated by comparing transition intensities in role-reinforced pairs (denoted q) versus role-reversed pairs (denoted q'), using bootstrapping ($n = 10\,000$).

To investigate how the temperamental difference between pair members influences pair performance, we awarded each pair a score of 1 for every trip out of cover that led to both pair members acquiring food, 0.5 when only one member acquired food and 0 when neither member acquired food. The average scoring rate (per minute) on each day was used as a measure of the joint efficiency of the pair, and we tested whether it was explained by the temperamental difference between pair members, using a generalized linear mixed model with training day as a random effect.

3. Results

To quantify individual movement rules, we modelled fish movement as a continuous-time Markov process, in which each fish could be either in cover or out foraging at any given time (figure 2). In both role-reinforced and role-reversed pairs, movement patterns were qualitatively similar to those observed in our previous works [15,25], in that both members of a pair were more likely to emerge from cover when their partner was out and to return when their partner was in cover, and these differences were in almost all cases

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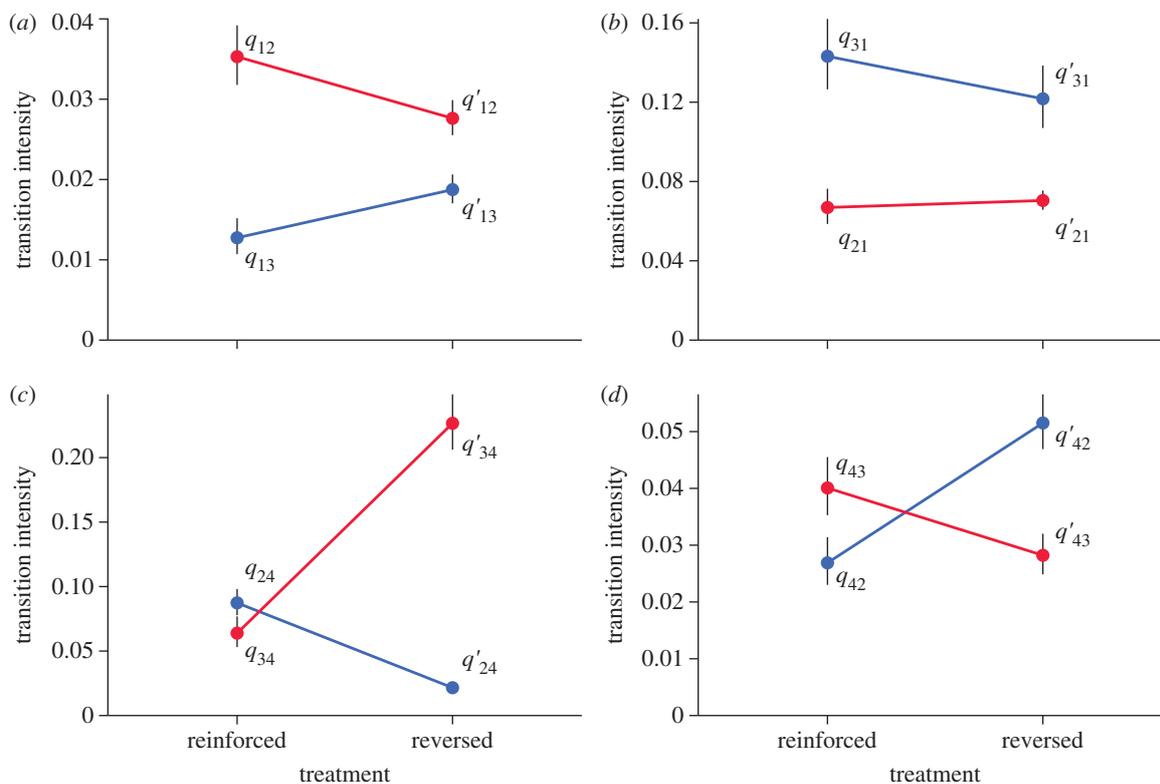
Figure 3. Transition intensities on the last day of the experiment estimated from the Markov model. Tendencies for bold (red circles) and for shy fish (blue circles) in control and role-reversed pairs to (a) initiate (q_{12} and q'_{12} for bold fish, q_{13} and q'_{13} for shy fish), (b) return (q_{21} and q'_{21} for bold fish, q_{31} and q'_{31} for shy fish), (c) join (q_{34} and q'_{34} for bold fish, q_{24} and q'_{24} for shy fish) and (d) abandon (q_{43} and q'_{43} for bold fish, q_{42} and q'_{42} for shy fish). Values are the best estimates (and 95% CIs).

significant (for bold fish in role-reinforced pairs, $q_{34} > q_{12}$, $p < 0.001$ and $q_{21} > q_{43}$, $p < 0.001$; for shy fish in role-reinforced pairs, $q_{24} > q_{13}$, $p < 0.001$ and $q_{31} > q_{42}$, $p < 0.001$; for bold fish in role-reversed pairs, $q'_{34} > q'_{12}$, $p < 0.001$ and $q'_{21} > q'_{43}$, $p < 0.001$; for shy fish in role-reversed pairs, $q'_{24} > q'_{13}$, $p = 0.170$ and $q'_{31} > q'_{42}$, $p < 0.001$). In other words, fish attend to one another's position and respond accordingly.

(a) Impact of experimental treatment on individual movement rules

Turning to the impact of treatment on movement patterns, we found that both bold and shy fish responded to the imposed reward scheme in the manner one might expect: bold fish showed a lesser tendency to lead (figure 3a; $q'_{12} < q_{12}$, $p = 0.039$) and a greater tendency to follow (figure 3c; $q'_{34} > q_{34}$, $p < 0.001$) in role-reversed compared with role-reinforced pairs (i.e. when they were rewarded for following rather than for leading); vice versa, shy fish showed a greater tendency to lead (figure 3a; $q'_{13} > q_{13}$, $p = 0.002$) and a lesser tendency to follow (figure 3c; $q'_{24} < q_{24}$, $p < 0.001$) in role-reversed compared with role-reinforced pairs (i.e. when they were rewarded for leading rather than for following).

Contradicting the predictions outlined in the Introduction [1,14,21,22–24], we did not find any difference in the adaptability of bold and shy individuals to changes in leadership. However, we did find that, for both bold and shy individuals, the tendency to lead is much less flexible than the tendency to follow. The tendency to initiate trips differed only between treatments by 27% in bold and 46% in shy fish (figure 3a; $q_{12}/q'_{12} = 1.27$ [95% CI: 1.01–1.59]; $q'_{13}/q_{13} = 1.46$ [1.14–1.91]), with virtually no difference in the tendency to return

to cover when out alone (figure 3b; $q'_{21}/q_{21} = 1.05$ [0.87–1.26]; $q_{31}/q'_{31} = 1.18$ [0.99–1.41]). By contrast, the tendency to join a partner out of cover (i.e. the act of following) differed much more remarkably between treatments. The bold fish was over three times faster to follow when cast in the role of follower rather than leader (figure 3c; $q'_{34}/q_{34} = 3.53$ [2.78–4.49]), and this change was much greater than that in leading ($q'_{34}/q_{34} > q_{12}/q'_{12}$, $p < 0.001$). Similarly, the shy fish cast in the role of a leader almost completely stopped following the bold (figure 3c; $q_{24}/q'_{24} = 4.07$ [3.23–5.07]), showing more flexibility than that in leading ($q_{24}/q'_{24} > q'_{13}/q_{13}$, $p < 0.001$). Analogous changes were seen in the tendency to abandon joint trips: a bold fish was much slower to abandon its partner when cast in the role of a follower rather than leader (figure 3d; $q_{43}/q'_{43} = 1.42$ [1.21–1.67]; $q_{43}/q'_{43} > q_{21}/q'_{21}$, $p = 0.012$), whereas a shy fish was much quicker to do so when cast in the role of a leader rather than a follower (figure 3d; $q'_{42}/q_{42} = 1.90$ [1.62–2.23]; $q'_{42}/q_{42} > q_{31}/q'_{31}$, $p < 0.001$).

In summary, fish (whether bold or shy) can easily learn to follow, but they cannot easily learn to lead. More precisely, temperamental differences in the tendency to follow are easily overridden by changes in the reward scheme (the red and blue lines cross in figure 3c,d), whereas temperamental differences in the tendency to lead are much more resistant to change (the red and blue lines do not cross in figure 3a,b).

(b) Collective performance

Lastly, turning from individual movement rules to collective performance (measured as the joint rate of food acquisition), we found that joint feeding rates were strongly affected by the
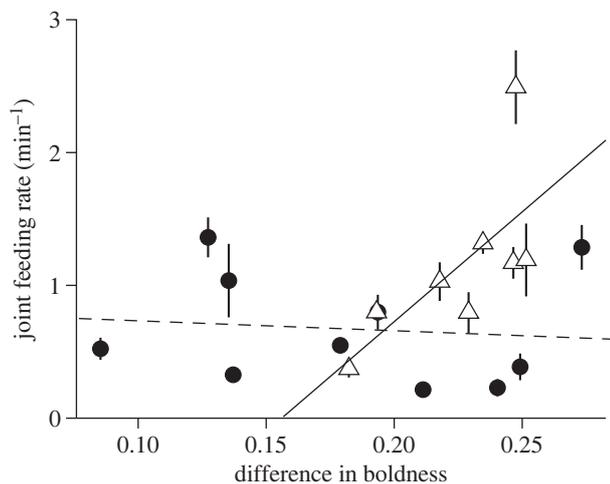
Figure 4. Joint feeding rate of fish pairs plotted against the difference in boldness between pair members. Open triangles represent average feeding rates over 4 days (± 1 s.e.) for the role-reinforced pairs, and the solid line the corresponding prediction of the best-fit linear model. Filled circles and the dashed line represent equivalent values for the role-reversed pairs.

difference in temperament between pair members, but that the effect differed between role-reinforced and role-reversed pairs ($\chi_1^2 = 18.20$, $p < 0.001$; figure 4). When natural roles were reinforced, pairs were more efficient at getting food if they consisted of individuals with very different temperaments (slope of performance on temperamental difference between pair members $= 16.53 \pm 3.87$ for role-reinforced pairs, estimate $\pm$ s.e.). By contrast, when roles were reversed, overall group efficiency was weakly negatively affected by temperament differences (slope of performance on temperamental difference between pair members $= -0.75 \pm 1.27$ for role-reversed pairs). In other words, temperamental differences within a pair led to improved performance when pair members were rewarded for assuming their usual roles, but to impaired performance when they were forced to switch roles.

4. Discussion

Our previous work on sticklebacks showed that temperamental differences in boldness strongly influence the adoption of leader and follower roles in foraging pairs. Bolder individuals typically lead, whereas shy individuals typically follow [15,25]. In this study, however, we have shown that both bolder and shyer fish can readily adjust their tendency to follow others in response to the profitability of doing so. Differences in the reward scheme we imposed overrode temperamental differences in the tendency to follow, such that bolder fish followed more assiduously than their partners in role-reversed pairs, just as shyer fish did in role-reinforced pairs. These findings are similar to the results of studies of social learning, in which individual reliance on social information use is modulated by the reliability of cues provided by others [31–33], and to the results of studies on social foraging, in which individual reliance on scrounging tactics (following others to obtain a share of the food they locate) is adjusted in response to its profitability [34,35].

On the face of it, our evidence for 'flexible following' suggests that leadership within a group is likely to prove

fluid, with switches in role occurring easily in response to changes in the information that different group members possess about the state of the environment [12]. Because there is greater profit to be gained by following group members who are better informed about the location of food sources, we would expect such individuals to emerge as leaders. However, our analysis also revealed that while the tendency to follow is malleable, the tendency to lead, or more precisely to initiate group movement, is much less flexible. Even after four days of training, differences in the reward scheme we imposed were not enough to overcome temperamental differences in the tendency to lead: bolder fish led more effectively than their partners in role-reinforced as well as in role-reversed pairs. It thus seems that the fish (whether bold or shy) can learn to follow but struggle to learn to lead.

Our finding that the tendency to follow is more malleable than the tendency to lead raises some intriguing questions about the evolution of animal personalities. To date, most models of personality evolution have focused on identifying selective pressures that could potentially explain the emergence of temperamental variation in a population [36]. However, our results suggest that different aspects of behaviour may be more or less sensitive to such variation, even in the same context (here social foraging). The fish in our experiments show consistent interindividual differences in the tendency to lead, which persist even in the face of our opposing training regimes, but no such robust differences in the tendency to follow. Why should one aspect of behaviour be less malleable than the other? Existing models suggest that certain kinds of feedback may promote or inhibit the emergence of distinct personality types in a population [36], but it remains to be seen whether such feedback mechanisms can account for the difference we observe between leading and following.

The inability of the fish to adjust their level of leadership (or initiative) in response to switches in social role also has interesting implications for the impact of personality differences on group performance. Studies of group psychology in humans have shown that groups featuring greater diversity in certain personality traits (principally extroversion) may enjoy improved performance [37,38], and there is some limited evidence for such effects also in non-human animals [39–41]. One explanation suggested in the human literature is that differences in extroversion can facilitate role differentiation and the emergence of leaders [37]. This idea is in accord with a recent model of leadership in animal groups, which suggests that selection for efficient coordination can drive the evolution of personality differences precisely because it promotes clear differentiation between leaders and followers within a group [3]. Yet the human data are far from consistent [42]. There is contradictory evidence from other studies that personality differences can sometimes have no effect, or even a negative effect, on team performance [43], and a recent meta-analysis found only weak effects of personality variation overall [44].

Our findings may help to account for these conflicting results on the impact of personality variation because they show that the effect of temperamental differences is likely to depend upon the roles that individuals adopt within a group. Figure 4 shows that the mean performance of fish pairs in our experiment was positively related to the difference in boldness between pair members when normal

social roles were reinforced. By contrast, when the fish were forced to switch roles, performance decreased with the difference in temperament between pair members because of the lack of flexibility in initiative. This suggests that strong positive effects of personality variation are only likely to emerge when members of a group are free to establish their own roles, such that bolder (or, in the human case, more extroverted) individuals can assume leadership. In this regard, it is interesting that some of the strongest positive results from human studies come from work on self-managed teams that do not have roles imposed on them but are free to structure their own work [45].

References

1. Couzin ID, Krause J, Franks NR, Levin SA. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)

2. King AJ, Johnson DDP, Van Vugt M. 2009 The origins and evolution of leadership. *Curr. Biol.* **19**, R911–R916. (doi:10.1016/j.cub.2009.07.027)

3. Johnstone RA, Manica A. 2011 Evolution of personality differences in leadership. *Proc. Natl Acad. Sci. USA* **108**, 8373–8378. (doi:10.1073/pnas.1102191108)

4. Peterson RO, Jacobs AK, Drummer TD, Mech LD, Smith DW. 2002 Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*. *Can. J. Zool.* **80**, 1405–1412. (doi:10.1139/z02-124)

5. Rands SA, Cowlishaw G, Pettifor RA, Rowcliffe JM, Johnstone RA. 2003 Spontaneous emergence of leaders and followers in foraging pairs. *Nature* **423**, 432–434. (doi:10.1038/nature01630)

6. Fischhoff IR, Sundaresan SR, Cordingley J, Larkin HM, Sellier MJ, Rubenstein DI. 2007 Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Anim. Behav.* **73**, 825–831. (doi:10.1016/j.anbehav.2006.10.012)

7. Barelli C, Boesch C, Heistermann M, Reichard UH. 2008 Female white-handed gibbons (*Hylobates lar*) lead group movements and have priority of access to food resources. *Behaviour* **145**, 965–981. (doi:10.1163/156853908784089243)

8. Conradt L, Krause J, Couzin ID, Roper TJ. 2009 'Leading according to need' in self-organizing groups. *Am. Nat.* **173**, 304–312. (doi:10.1086/596532)

9. Sueur C, Deneubourg J-L, Petit O, Couzin ID. 2010 Differences in nutrient requirements imply a non-linear emergence of leaders in animal groups. *PLoS Comput. Biol.* **6**, e1000917. (doi:10.1371/journal.pcbi.1000917)

10. McClure M, Ralph M, Despland E. 2011 Group leadership depends on energetic state in a nomadic collective foraging caterpillar. *Behav. Ecol. Sociobiol.* **65**, 1573–1579. (doi:10.1007/s00265-011-1167-5)

11. Nakayama S, Johnstone RA, Manica A. 2012 Temperament and hunger interact to determine the emergence of leaders in pairs of foraging fish. *PLoS ONE* **7**, e43747. (doi:10.1371/journal.pone.0043747)

12. Reebs SG. 2000 Can a minority of informed leaders determine the foraging movements of a fish shoal? *Anim. Behav.* **59**, 403–409. (doi:10.1006/anbe.1999.1314)

13. Faria JJ, Dyer JRG, Tosh CR, Krause J. 2010 Leadership and social information use in human crowds. *Anim. Behav.* **79**, 895–901. (doi:10.1016/j.anbehav.2009.12.039)

14. Flack A, Pettit B, Freeman R, Guilford T, Biro D. 2012 What are leaders made of? The role of individual experience in determining leader–follower relations in homing pigeons. *Anim. Behav.* **83**, 703–709. (doi:10.1016/j.anbehav.2011.12.018)

15. Harcourt JL, Ang TZ, Sweetman G, Johnstone RA, Manica A. 2009 Social feedback and the emergence of leaders and followers. *Curr. Biol.* **19**, 248–252. (doi:10.1016/j.cub.2008.12.051)

16. Leca JB, Gunst N, Thierry B, Petit O. 2003 Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Anim. Behav.* **66**, 1045–1052. (doi:10.1006/anbe.2003.2276)

17. Jacobs A, Maumy M, Petit O. 2008 The influence of social organisation on leadership in brown lemurs (*Eulemur fulvus fulvus*) in a controlled environment. *Behav. Process.* **79**, 111–113. (doi:10.1016/j.beproc.2008.05.004)

18. Stueckle S, Zinner D. 2008 To follow or not to follow: decision making and leadership during the morning departure in Chacma baboons. *Anim. Behav.* **75**, 1995–2004. (doi:10.1016/j.anbehav.2007.12.012)

19. Lewis JS, Wartzok D, Heithaus MR. 2011 Highly dynamic fission-fusion species can exhibit leadership when traveling. *Behav. Ecol. Sociobiol.* **65**, 1061–1069. (doi:10.1007/s00265-010-1113-y)

20. Dugatkin LA. 1991 Dynamics of the tit for tat strategy during predator inspection in the guppy (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* **29**, 127–132. (doi:10.1007/BF00166487)

21. Harcourt JL, Sweetman G, Manica A, Johnstone RA. 2010 Pairs of fish resolve conflicts over coordinated movement by taking turns. *Curr. Biol.* **20**, 156–160. (doi:10.1016/j.cub.2009.11.045)

22. Wolf M, Van Doorn GS, Weissing FJ. 2011 On the coevolution of social responsiveness and behavioural consistency. *Proc. R. Soc. B* **278**, 440–448. (doi:10.1098/rspb.2010)

23. Beauchamp G. 2000 Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour* **137**, 301–314. (doi:10.1163/156853900502097)

24. Kurvers RHJM, Prins HHT, van Wieren SE, van Oers K, Nolet BA, Ydenberg RC. 2010 The effect of personality on social foraging: shy barnacle geese scrounge more. *Proc. R. Soc. B* **277**, 601–608. (doi:10.1098/rspb.2009.1474)

25. Nakayama S, Harcourt JL, Johnstone RA, Manica A. 2012 Initiative, personality and leadership in pairs of foraging fish. *PLoS ONE* **7**, e36606. (doi:10.1371/journal.pone.0036606)

26. Dall SRX, Houston AI, McNamara JM. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739. (doi:10.1111/j.1461-0248.2004.00618.x)

27. Borg B, Bornestaf C, Hellqvist A, Schmitz M, Mayer I. 2004 Mechanisms in the photoperiodic control of reproduction in the stickleback. *Behaviour* **141**, 1521–1530. (doi:10.1163/1568539042948213)

28. Harcourt JL, Sweetman G, Johnstone RA, Manica A. 2009 Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. *Anim. Behav.* **77**, 1501–1505. (doi:10.1016/j.anbehav.2009.03.004)

29. Harcourt JL, Biau S, Johnstone R, Manica A. 2010 Boldness and information use in three-spined sticklebacks. *Ethology* **116**, 440–447. (doi:10.1111/j.1439-0310.2010.01757.x)

30. Kurvers RHJM, Eijkelenkamp B, van Oers K, van Lith B, van Wieren SE, Ydenberg RC, Prins HHT. 2009 Personality differences explain leadership in barnacle geese. *Anim. Behav.* **78**, 447–453. (doi:10.1016/j.anbehav.2009.06.002)

31. Laland K. 2004 Social learning strategies. *Learn. Behav.* **32**, 4–14. (doi:10.3758/BF03196002)

32. Pike TW, Laland KN. 2010 Conformist learning in nine-spined sticklebacks' foraging decisions. *Biol. Lett.* **6**, 466–468. (doi:10.1098/rsbl.2009.1014)

33. Morgan TJH, Rendell LE, Ehn M, Hoppitt W, Laland KN. 2012 The evolutionary basis of human social learning. *Proc. R. Soc. B* **279**, 653–662. (doi:10.1098/rspb.2011.1172)

34. Giraldeau L-A, Lefebvre L. 1986 Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Anim.*

Behav. **34**, 797 – 803. (doi:10.1016/S0003-3472(86)80064-1)

35. Morand-Ferron J, Giraldeau L-A. 2010 Learning behaviorally stable solutions to producer – scrounger games. *Behav. Ecol.* **21**, 343 – 348. (doi:10.1093/beheco/arp195)

36. Dingemanse NJ, Wolf M. 2010 Recent models for adaptive personality differences: a review. *Phil. Trans. R. Soc. B* **365**, 3947 – 3958. (doi:10.1098/rstb.2010.0221)

37. Neuman GA, Wagner SH, Christiansen ND. 1999 The relationship between work-team personality composition and the job performance of teams. *Gr. Organ. Manage.* **24**, 28 – 45. (doi:10.1177/1059601199241003)

38. Mohammed S, Angell LC. 2003 Personality heterogeneity in teams: which differences make a

difference for team performance? *Small Gr. Res.* **34**, 651 – 677. (doi:10.1177/1046496403257228)

39. Dyer JRG, Croft DP, Morrell LJ, Krause J. 2008 Shoal composition determines foraging success in the guppy. *Behav. Ecol.* **20**, 165 – 171. (doi:10.1093/beheco/arn129)

40. Pruitt JN, Riechert SE. 2011 How within-group behavioural variation and task efficiency enhance fitness in a social group? *Proc. R. Soc. B* **278**, 1209 – 1215. (doi: 10.1098/rspb.2010.1700)

41. Modlmeier AP, Liebmann JE, Foitzik S. 2012 Diverse societies are more productive: a lesson from ants. *Proc. R. Soc. B* **279**, 2142 – 2150. (doi:10.1098/rspb.2011.2376)

42. Bell ST. 2007 Deep-level composition variables as predictors of team performance: a meta-analysis.

J. Appl. Psychol. **92**, 595 – 615. (doi:10.1037/0021-9010.92.3.595)

43. Halfhill T, Sundstrom E, Lahner J, Calderone W, Nielsen TM. 2005 Group personality composition and group effectiveness. *Small Gr. Res.* **36**, 83 – 105. (doi:10.1177/1046496404268538)

44. Peeters MAG, Tuijl van HFJM, Rutte CG, Reymen IMMJ. 2006 Personality and team performance: a meta-analysis. *Eur. J. Pers.* **20**, 377 – 396. (doi:10.1002/per.588)

45. Humphrey SE, Hollenbeck JR, Meyer CJ, Ilgen DR. 2011 Personality configurations in self-managed teams: a natural experiment on the effects of maximizing and minimizing variance in traits. *J. Appl. Soc. Psychol.* **41**, 1701 – 1732. (doi:10.1111/j.1559-1816.2011.00778.x)