

Pairs of Fish Resolve Conflicts over Coordinated Movement by Taking Turns

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Summary

When individuals stand to gain by interacting with one another, but disagree over their preferred course of collective action, coordination can be hard to achieve [1–4]. In previous work, we found that pairs of stickleback fish prefer to synchronize their trips out of cover to look for food [5], possibly because this reduces perceived predation risk [6]. To create a degree of conflict over group coordination, we trained individual fish to expect food at one of two alternative, exposed locations and paired individuals with different expectations. Compared with isolated individuals, members of a pair showed a significantly increased tendency to alternate between foraging sites, together taking turns to visit first one individual's favored site and then the other individual's. Using a Markov-chain model to infer the individual rules underlying their joint behavior, we found that fish respond to a partner that breaks the pattern of alternation by themselves reverting to less regular behavior. Our results confirm theoretical predictions that conflict over group coordination can be resolved by taking turns [7–10] and show that, in this system, the pattern of alternation is actively monitored and maintained.

Results and Discussion

During a three-day training period, individual sticklebacks were placed for one hour per day in a long rectangular tank. In the center of the tank was a “safe” resting area (deep water with weed cover, which is preferred by resting individuals [5]) from which the fish could venture out to visit “exposed” areas (shallow water with no shelter) at either end of the tank (Figure 1). Each fish was then independently trained to expect delivery of food at one end of the tank only. For two days after the training period, fish were observed for an hour each day in the absence of food delivery to record their individual behavior. During this time, they made significantly more trips out of cover to the end of the tank where they had been trained to expect food (median, 45 trips h^{-1} ; interquartile range, 32.5–64.0), although they continued to visit the other end as well (33.5 trips h^{-1} ; 27.0–49.0; Wilcoxon pair test, $V = 962.5$ and $p < 0.001$). Previous work had revealed that individual fish differ consistently in their willingness to emerge from cover (“boldness” [11–16]), and that bolder and less bold individuals behave differently in a pair [5]. Consequently, we also recorded the boldness of each fish during these hours of observation, measured as the proportion of time spent out of cover (median, 48.3% [27.9%–57.8%]).

We then randomly paired fish that had been trained to expect food at opposite ends of the tank. Over the course of four days, each pair was placed for one hour a day in a tank that had been divided lengthwise by a plastic partition to create two long compartments (with one fish in each). We alternated between the use of transparent and opaque partitions on successive days, allowing us to compare the behavior of the fish when they were and were not able to observe each other's movements. When the members of a pair could not observe one another, the bolder fish made 105.0 (71.8–111.0) trips out of cover and spent 66.0% (60.3%–71.5%) of its time exposed, whereas the less bold individual made 85.5 (48.3–102.8) trips and spent 55.6% (33.7%–62.7%) of its time exposed. Fish boldness levels were consistent with the values observed during the posttraining assessment period (correlation between posttraining and experimental boldness, $r_{21} = 0.715$, $p < 0.001$). Both fish, as in the posttraining assessment period, made more trips out of cover in the direction in which they had been trained to look for food: 57.4% (53.7%–60.7%) of trips in the case of the bolder member of the pair and 57.9% (52.6%–62.3%) of trips in the case of the less bold individual (no significant difference in directional bias between the two; paired $V = 145$, $p = 0.559$).

When they were able to observe one another through a transparent partition, the bolder fish made 113.0 (104.0–171.2) trips out of cover and spent 74.0% (70.8%–76.9%) of its time exposed, whereas the less bold individual made 113.0 (78.0–125.0) trips and spent 72.1% (69.0%–73.0%) of its time exposed. There was a decrease in the difference between the proportions of time that the two fish in a pair spent out of cover, compared with the opaque treatment (reduced median difference in proportion of time out between members of a pair, transparent versus opaque, paired $V = 853$, $p < 0.001$), and the fish tended to make their excursions together (quantifiable by a measure of coordination analogous to genetic linkage disequilibrium [17]; coordination scores computed for transparent versus opaque, paired $V = 0$, $p < 0.001$), as shown in Figure 2A.

How was the conflict over preferred foraging direction resolved? When fish in a pair could observe one another, the bolder individual made 54.4% (50.3%–56.4%) and the less bold individual made 53.0% (49.9%–56.4%) of its trips in the direction in which it had been trained to look for food. Both thus showed a significant decrease in their individual bias toward their own preferred end of the tank, in comparison with their behavior when they could not see each other (see Figure S1A available online; proportion of trips out of cover to preferred end of the tank, transparent versus opaque, paired $V = 831$, $p = 0.001$), with no difference in bias between the bolder and less bold member of the pair (paired $V = 171$, $p = 0.329$). Moreover, when averaging across pairs, there was no net bias in directional preference (proportion of joint trips out of cover in the direction preferred by the bolder fish, one-sample Wilcoxon for $\mu \neq 0.5$, $V = 152$, $p = 0.690$; Figure 2B; note that any trip out of cover by one fish during which it was joined by the other fish prior to returning to cover was counted as a joint trip).

This “fair” resolution of conflict was achieved by the fish together increasing their tendency to take turns visiting

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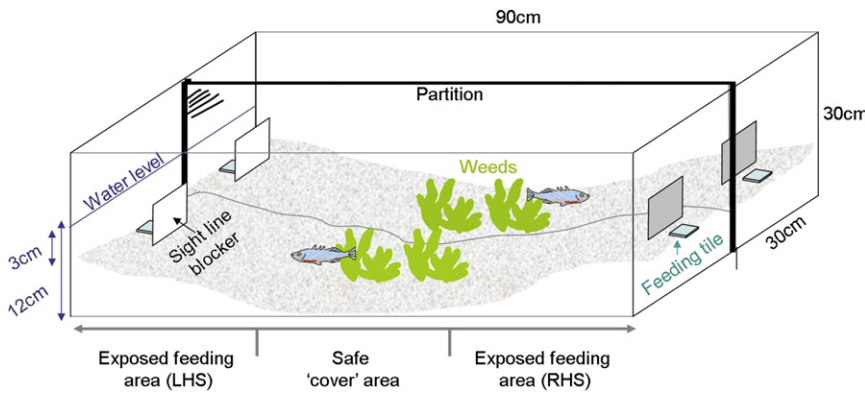


Figure 1. Diagrammatic Representation of the Experimental Set-Up

opposite ends of the tank. Although some tendency to avoid visiting the same end of the tank twice in a row could be detected in fish that were visually isolated (proportion of trips out of cover in opposite direction to last trip, 60.2% [53.4%–66.7%]), members of a pair who could see one another showed a significantly enhanced tendency to make consecutive trips out of cover in opposite directions (proportion of trips out of cover in opposite direction to last trip, 67.2.4% [60.9%–73.7%]; transparent versus opaque, paired $V = 166$, $p < 0.001$; Figure S1B; estimates for bolder and less bold were pooled as there was no difference between them, paired $V = 142$, $p = 0.917$). Although both fish were overall equally likely to initiate joint trips (proportion of joint trips initiated by bolder, 52.9% [44.0%–60.9%], $\mu \neq 0.5$, $V = 171.5$, $p = 0.315$), each fish was more likely to initiate joint trips in its preferred direction (proportion of joint trips initiated in preferred direction, pooled for both pair members, 54.4% [47.1%–61.8%], $\mu \neq 0.5$, $V = 703$, $p = 0.015$) with no difference between bolder and less bold in this bias (paired $V = 114$, $p = 0.482$). The less bold fish tended to terminate a greater proportion of joint trips than did the bolder individual (57.1% [47.5%–66.7%], $\mu \neq 0.5$, $V = 78.5$, $p = 0.076$), with both members of the pair terminating more joint trips in their less preferred direction (pooled, 57.2% [49.4%–64.9%], $\mu \neq 0.5$, $V = 708$, $p = 0.001$; no difference between bolder and less bold, paired $V = 189$, $p = 0.126$).

To examine in more detail how turn-taking emerges and is maintained, we fitted continuous-time Markov Chain models to the movements of each pair of fish, both when separated by an opaque and by a transparent partition. In these models,

and 48 possible transitions between pair states, corresponding to movement of one fish or the other between locations. Best-fit transition intensities between the various states are shown in Figure 3. We found that when the fish could see one another, they changed their behavior significantly in response to one another's movements; a constrained model that ruled out such responses, and specified transition intensities independently for each individual, gave a much inferior fit by comparison with the full, unconstrained model (log-likelihood ratio test, $\chi^2_{120} = 849.0$, $p < 0.001$). In contrast, when the fish could not see one another, the constrained model (shown in Figure 3A) gave a better fit (test for unconstrained model being more informative than constrained model, $\chi^2_{120} = 1.1$, $p > 0.9$).

We investigated differences in individual behavior (e.g., tendency to go in the preferred direction versus the nonpreferred direction) by comparing appropriate transition intensities. For a pair of fish that could see each other, q_{ij} denotes the transition intensity from pair state i to pair state j (Figure 3B); for a pair of fish that could not see each other, b_{ij} denotes transition intensities from individual state i to individual state j for the bolder fish, and s_{ij} for the less bold fish (Figure 3A). A formal test can be performed by bootstrapping, looking for deviations from unity in the ratios of the transition intensities of interest. Bootstrap tests revealed that, even when fish could not see one another, both members of a pair were significantly more likely to leave cover in the opposite direction to their last trip out, if they had last gone in their less preferred direction (for the bolder, $b_{2,3}/b_{2,4} = 1.35$ [1.30–1.39], $p = 0.001$; for the less bold, $s_{1,4}/s_{1,3} = 1.33$ [1.26–1.45],

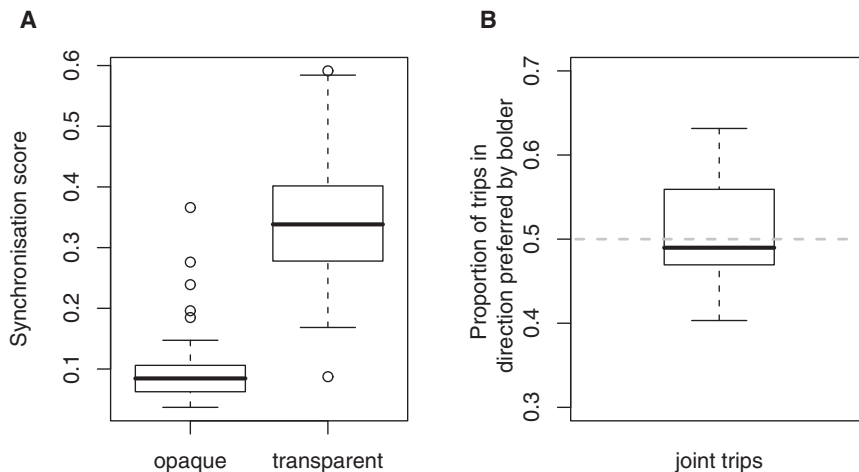


Figure 2. Pair Behavior

(A) Pair coordination scores for experiments with an opaque barrier (when fish could not see each other) and a transparent barrier (when they could see each other).

(B) The lack of a directional bias in the number of joint trips in the direction preferred by the bold fish; see also Figure S1. Lines, boxes, error bars, and circles show medians, interquartile ranges, minima and maxima (excluding outliers), and outliers (which deviate from the median by >1.5 times the interquartile range), respectively.

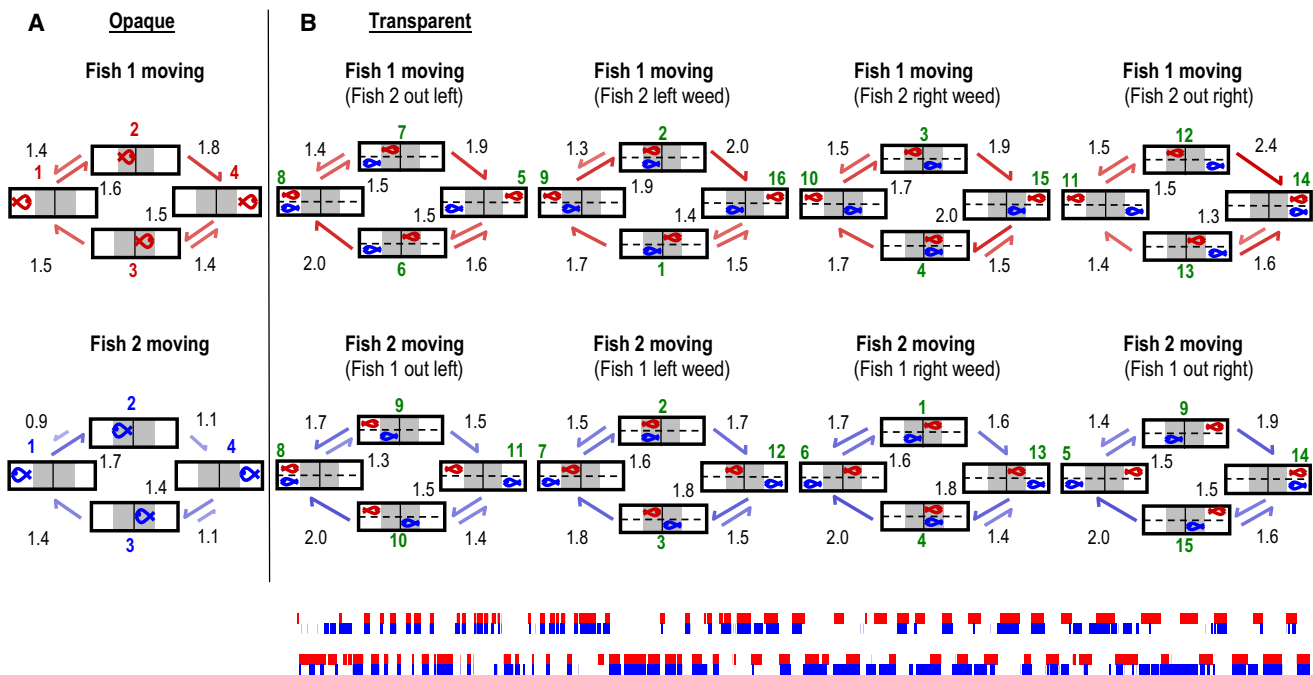


Figure 3. Individual Movement Rules

Transition intensities for individuals (A) moving between the four possible states (red and blue for bolder and less bold fish, respectively) during the experiment using opaque partitions and (B) moving between possible states for each pair (green) when transparent partitions were used. The area in which fish were covered by weed is shown in gray; the exposed area is shown in white. The bolder fish and associated transitions are shown in red, and the less bold fish and associated transitions are shown in blue. The length and color gradation of each arrow is proportional to the magnitude of the relevant transition intensity. Below the diagram of pair transitions, we show an illustrative set of results from one pair (with a transparent partition): time runs from left to right. Periods during which the bolder fish was out of cover are indicated by red shading, and periods when the less bold fish was out are in blue. The height of the shading indicates on which side of the covered area the fish in question emerged. See also Figure S2.

$p = 0.001$), but this was not the case after visiting their preferred end of the tank (bolder, $b_{1,4}/b_{1,3} = 1.06$ [1.03–1.09], $p = 0.069$; less bold, $s_{2,3}/s_{2,4} = 1.03$ [0.99–1.08], $p = 0.293$). When the fish could see one another, their behavior varied according to their recent experience. Pairs that had not yet established or had lost coordination, and whose most recent trips out of cover were to opposite ends of the tank, showed no greater tendency to alternate the direction of their trips out than when they could not see one another (for bolder, after trips in the least preferred direction, $q_{3,15}/q_{3,10} = 1.36$ [1.24–1.55] versus $b_{2,3}/b_{2,4}$, $p = 0.457$; after trips in the preferred direction, $q_{1,9}/q_{1,16} = 1.05$ [1.01–1.11] versus $b_{1,4}/b_{1,3}$, $p = 0.528$; for less bold, after trips in the least preferred direction, $q_{3,7}/q_{3,12} = 1.25$ [1.14–1.35] versus $s_{1,4}/s_{1,3}$, $p = 0.703$; after trips in the preferred direction, $q_{1,13}/q_{1,6} = 0.97$ [0.92–1.03] versus $s_{2,3}/s_{2,4}$, $p = 0.709$). However, if one fish left cover alone in the preferred direction of its partner, the latter was then significantly more likely to visit the same end of the tank, regardless of the direction of its previous trip (bolder joining the less bold on its preferred side, after a trip in the opposite direction, $q_{12,14}$ versus $b_{2,3}$, 1.50 [1.35–1.65], $p = 0.009$; after a trip in the same direction: $q_{13,14}$ versus $b_{1,3}$, 1.23 [1.15–1.30], $p = 0.012$; less bold joining the bolder in its preferred direction, after a trip in the opposite direction, $q_{9,8}$ versus $s_{2,4}$, 1.74 [1.61–1.88], $p < 0.001$; after a trip in the same direction: $q_{10,8}$ versus $s_{1,4}$, 1.77 [1.66–1.88], $p < 0.001$), thus establishing or restoring coordination.

Once coordination was established, fish whose most recent trips out of cover were to the same end of the tank were significantly more likely to alternate the direction of subsequent

excursions (by comparison with fish that could see one another but whose most recent trips were to opposite ends of the tank; for bolder, after joint trips in the least preferred direction, $q_{2,16}/q_{2,9} = 1.65$ [1.54–1.78] versus $q_{3,15}/q_{3,10}$, $p < 0.001$; after trips in the preferred direction, $q_{4,10}/q_{4,15} = 1.21$ [1.15–1.25] versus $q_{1,9}/q_{1,16}$, $p = 0.015$; for less bold, after joint trips in the least preferred direction, $q_{4,6}/q_{4,13} = 1.60$ [1.49–1.71] versus $q_{3,7}/q_{3,12}$, $p = 0.059$; after trips in the preferred direction, $q_{2,12}/q_{2,7} = 1.17$ [1.12–1.22] versus $q_{1,13}/q_{1,6}$, $p = 0.040$). This propensity for “taking turns” helped to maintain coordinated movement, although all pairs tended occasionally to lose (and subsequently regain) coordination for short periods of time, as seen in the illustrative set of results in Figure 3.

Our results show that animals, like humans [18–20], can solve conflicts over group coordination by taking turns to jointly visit each individual’s preferred site. This pattern of alternation is established and maintained (with occasional lapses) by individual response to the immediate history of coordination within a pair. The Markov Chain analysis allows us to infer these individual responses, which are similar to those predicted by the hypothetical turn taking with independent randomization (TTIR) strategy derived by Lau and Mui in their analysis of the repeated Battle of the Sexes game [10], in that fish exhibit a significantly increased tendency to alternate only once they have achieved coordination (see [8–10] for further theoretical analyses of turn-taking). Prior to the establishment of this turn-taking phase, or when it is interrupted by a breakdown in coordination, they show no greater tendency to alternate between potential options than they would in isolation and instead display a clear bias in favor of their own “preferred” option.

The turn-taking we observed in this experiment contrasts markedly with the outcome of a previous study in which only a single foraging site was available. In that case, the bolder fish in a pair emerged as a consistent leader, initiating the majority of joint trips out of cover [5], whereas in the present study, the two fish in each pair instead “shared” leadership, initiating the same number of joint trips but each tending to lead trips in its preferred direction. These findings confirm the importance of Conrard and Roper’s [21] distinction between conflict over synchronization of activities (i.e., timing) and conflict over alternative destinations. Our results also suggest that, to fully understand the dynamics of collective decisions, we need to consider repeated interactions over time. Democracy need not imply that every decision reflects a compromise among members of a group. Rather, with one temporary leader regularly trading places with another, turn-taking ensures, over time, an average outcome that is fair.

Experimental Procedures

Study Organism and Equipment

A stock of three-spined sticklebacks (*Gasterosteus aculeatus*) was collected with sweep nets from the Swaffham Bulbeck area of the River Cam (United Kingdom) during 2007 and kept in a laboratory 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. Fish were taken from one population, because variation in boldness may be influenced by evolutionary history [12].

Fish were housed in large glass aquaria with dual filtration systems (external Hagen and undergravel filters) that were lined with gravel and contained a number of plastic plants (Hagen). Sticklebacks were not sexed, but the standard laboratory temperature used prevented them from coming into breeding condition [22]. All fish used in experiments were of similar length (45 ± 5 mm from tip of snout to caudal peduncle) to remove size as a potentially confounding variable [23]. All sticklebacks were fed to satiation daily on frozen bloodworms (Chironomid larvae), and experiments were approved by the Animal Users Management Committee of the University of Cambridge.

Experimental Set-Up

Fish to be trained for experiments were moved to partitioned holding tanks ($60 \times 30 \times 40$ cm). Each glass tank held six fish in individual compartments that were separated by a transparent plastic divide. Undergravel filtration operated over the whole system, and each compartment had a plastic plant at one end and a white plastic tile (~ 1.5 cm²) placed on the gravel at the other. These tanks allowed individual fish identification but minimized any stress caused by isolation.

During training, fish were transferred to glass experimental tanks ($90 \times 30 \times 30$ cm; Figure 1). The walls of these were covered with black opaque plastic to prevent external movement from being seen by the fish. Each tank was partitioned lengthwise with either an opaque or transparent plastic barrier to form two long compartments. The tanks were lined with white gravel in such a way that slopes were created from a deep central weeded area (containing two plastic plants) with water depth of 12 cm to shallow feeding ends, of water depth 2 cm, at either end of the tank. A feeding tile, similar to those used in the holding tanks, was placed at either end behind small plastic screens (8×8 cm visible above the gravel, one white and one gray), which prevented fish from seeing food from the deep weeded center of the tank.

When fish were not present in the tanks, a bubbled supply of air was provided to these experimental tanks to maintain aeration of the water.

After fish were given 5 min acclimation time in the test environment, their behavior was recorded with a Sony DCR-35E digital video camera mounted directly above the tank and aligned to give a full view of the whole set-up.

Training and Assessment of Individual Temperament

Data were collected in fortnightly cycles, with fish spending 1 hr each weekday in the experimental tanks for either training or experimental purposes. The first three days of a cycle were used for training performed with opaque barriers in place to prevent visual contact between fish. Before each hour-long session, a single medium-sized bloodworm was placed onto either the right or left feeding tile. Fish were individually moved from the

holding tanks to the weedy center of an experimental tank. After 30 min, tanks were inspected, and a second bloodworm was placed on the feeding tile if the first had been consumed. Any fish that failed to consume two bloodworms on any given day was fed in the holding tanks after training to ensure that all received and ate two bloodworms each day.

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 by videotaping 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 because feeding could influence foraging tendencies; fish were fed a single bloodworm each upon being returned to the holding tanks. Over the weekend, sticklebacks were not trained but were left in their individual holding tanks and fed a single bloodworm each day.

Interaction between Pairs of Individuals

Assessed fish were given an additional day of training at the start of the second week, having not been exposed to food in the experimental tanks over the four previous days. Fish were assigned to pairs, so that each pair contained individuals trained in different directions, and treatments for the four experimental days alternated the use of transparent and opaque barriers to assess the response to a foraging partner. No food was given each day until after the tests had been completed.

Data Analysis

Videos were transferred from DV tape to DVD and were watched back at four times the normal speed. The timings of all transitions into and out of cover in the different directions were recorded with a custom-designed data logger. From this information, we also computed the number of and the time spent on trips in each direction by either fish.

To assess the how fish responded to each other, we fitted a continuous-time MCMC model [24] in which each fish could be in one of four states (either exposed in its preferred or in less preferred direction or under cover—i.e., to some degree obscured by weeds—after a trip in either its preferred or less preferred direction). This gave a model with 16 states (Figure S1) describing all possible combinations of individual states of the pair, with 64 possible transitions. The temperament of each fish was quantified as the log of the ratio between the time spent out of cover over the time spent under cover during the boldness assessments prior to the main experiments. The fish with a higher temperament score within the pair was termed “bolder,” and the fish with a lower score was termed “less bold.” The scores for the two fish in each pair were fitted as covariates to the MCMC model to account for the inherent difference in activity level of the fish used in the experiments. Confidence intervals on the parameters of the MCMC (both transition intensities and covariates) were obtained by taking 1000 bootstraps and refitting the model to the resampled data.

To test whether the fish responded to each other’s behavior, we created a simpler model in which transition intensities for each fish were not affected by the position of its partner (this could be achieved by constraining the appropriate intensities to be equal to each other). The reduced model was then compared to the full model via a log-likelihood ratio test, which follows a χ^2 distribution with degrees of freedom equal to the difference in number of parameters between the two models. All models were fitted with the package *msm* v0.8.2 (written by Christopher Jackson) in R 2.8.1 (R Core Development Team).

Supplemental Information

Supplemental Information includes two figures and can be found with this article online at [doi:10.1016/j.cub.2009.11.045](https://doi.org/10.1016/j.cub.2009.11.045).

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