

Consensus Decision Making by Fish

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Summary

Decisions reached through consensus are often more accurate, because they efficiently utilize the diverse information possessed by group members [1–3]. A trust in consensus decision making underlies many of our democratic political and judicial institutions [4], as well as the design of web tools such as Google, Wikipedia, and prediction markets [5, 6]. In theory, consensus for the option favored by the majority of group members will lead to improved decision-making accuracy as group size increases [2, 4]. Although group-living animals are known to utilize social information [7–10], little is known about whether or not decision accuracy increases with group size. In order to reach consensus, group members must be able to integrate the disparate information they possess. Positive feedback, resulting from copying others, can spread information quickly through the group, but it can also result in all individuals making the same, possibly incorrect, choice [8, 11, 12]. On the other hand, if individuals never copy each other, their decision making remains independent and they fail to benefit from information exchange [4]. Here, we show how small groups of sticklebacks (*Gasterosteus aculeatus*) reach consensus when choosing which of two replica fish to follow. As group size increases, the fish make more accurate decisions, becoming better at discriminating subtle phenotypic differences of the replicas. A simple quorum rule proves sufficient to explain

our observations, suggesting that animals can make accurate decisions without the need for complicated comparison of the information they possess. Furthermore, although submission to peers can lead to occasional cascades of incorrect decisions, these can be explained as a byproduct of what is usually accurate consensus decision making.

Results and Discussion

To investigate consensus decision making, we presented groups of three-spined sticklebacks (*Gasterosteus aculeatus*; a common freshwater fish) with images of conspecifics with differing phenotypic traits. An individual's appearance can convey information to, and thus have important fitness consequences for, an observer [7]. For example, abdomen profile can imply foraging success, whereas color may relate to fishes' health and small black spots could indicate infestation by a parasite. In our experiment, we chose four phenotypes that were likely to convey information: size, corpulence, shade, and spottiness. Eleven different images were created, depicting small, medium, or large; fat, medium, or thin; light, medium, or dark; and spotted or plain (see [Experimental Procedures](#)). In each trial, we presented the focal fish with a choice between two replicas with different traits.

[Figure 1](#) gives the distribution of the number of fish following the more attractive replica fish for experimental trials with one, two, four, and eight fish and the large versus medium and dark versus light treatments. For single individuals, one of the replicas was always more attractive (in the sense that it was followed more often) than the other. This bias was preserved as group size increased, with the majority of fish following the image that was more attractive in the single fish trials. As group size increases, the distribution of the number of fish following the popular leader takes a J shape (test of fit of a binomial distribution is significant to $p < 0.001$ for all treatments for group sizes of four and eight). In the majority of trials, either all or all but one of the fish followed the more attractive leader, whereas in a substantial minority of trials, all or all but one of the fish followed the least attractive leader. Similar results were seen across all experimental treatments (see [Figure S2](#), available online): fish in the same trial tend to follow the same leader, and the proportion of fish following the more attractive leader increases with group size. These J-shaped distributions are characteristic of positive feedback and copying [11, 13, 14].

In order to make more concrete statements about the type of decision making occurring in these groups, we give three alternative hypotheses about the probability that a fish in a group of size n with replica treatment j will follow the more attractive replica in that treatment, p_{nj} , as well as the probability that all fish follow the more attractive replica, a_{nj} . Specifically, we hypothesize relationships between p_{nj} and a_{nj} and the probability that a fish on its own follows the more attractive replica, p_{1j} .

Independent Decision

Each fish decides which replica to follow independent of the other fish. Under this hypothesis, the proportion of fish

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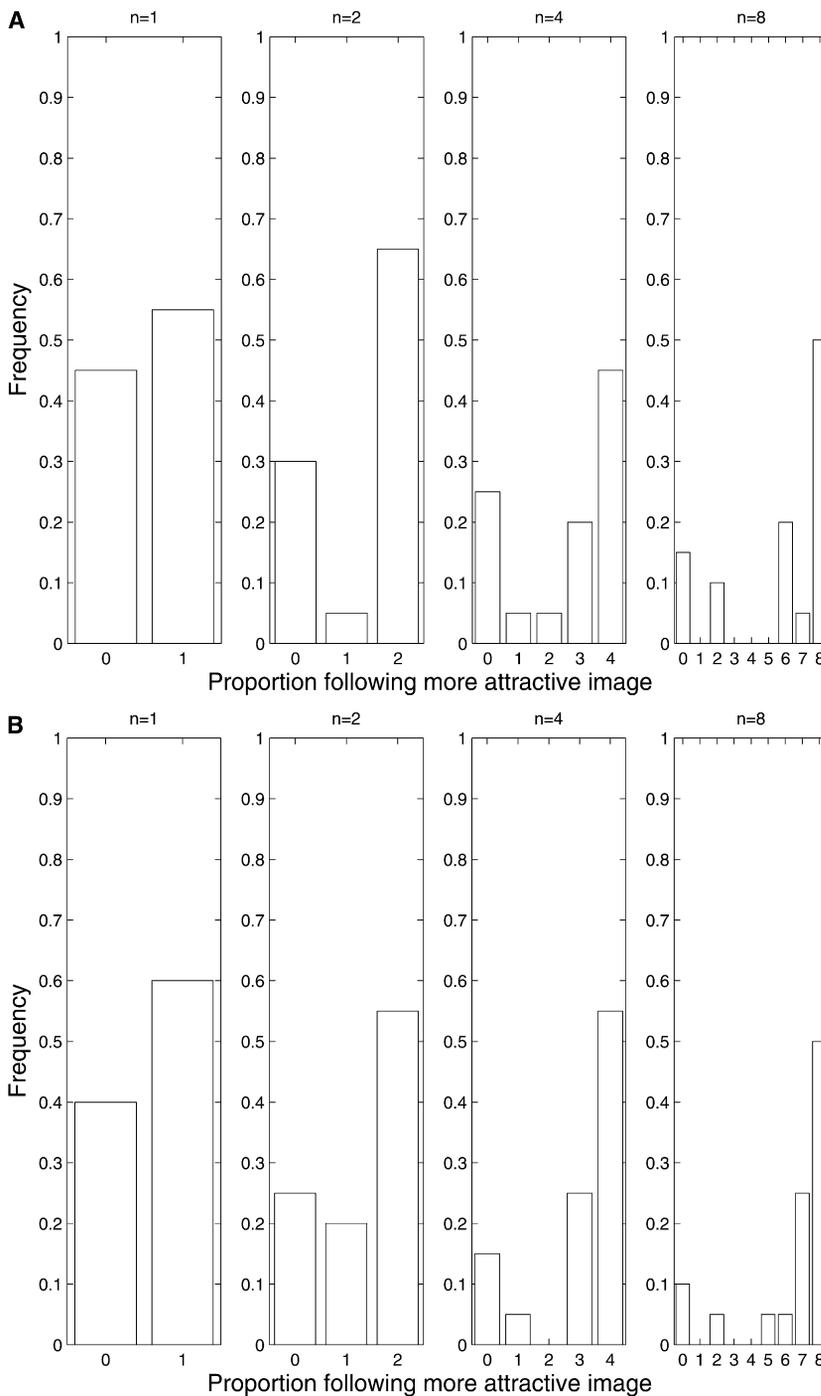


Figure 1. Distribution over All Trials for the Number of Fish Following the More Attractive Leader
(A) Distribution is shown for the large-versus-medium treatment.
(B) Distribution is shown for the dark-versus-light treatment.
See Figure S1 for the same figures for all other experimental treatments.

“Condorcet” Decision

Here, we assume that each group member initially has a preference for one of the two replicas, such that their probability of “preferring” to follow the more attractive replica is equal to p_{1j} . We then assume that the group as a whole follows the preferred direction of the majority of its members, such that

$$p_{nj} = a_{nj} = \sum_{i=n/2+1}^n \binom{n}{i} p_{1j}^i (1-p_{1j})^{n-i} + \frac{1}{2} \binom{n}{n/2} p_{1j}^{n/2} (1-p_{1j})^{n/2}.$$

This is a version of Condorcet’s majority decision-making theory [4]. A Condorcet decision is a perfect consensus decision, in the sense that given the information available to the fish, it is the maximum probability that they follow the most attractive replica.

Figure 2 shows how the theoretical values of p_{nj} and a_{nj} change with group size and number of trials, respectively, for independent, aggregated, and Condorcet decisions. These are compared to the mean and standard deviation across all experimental treatments of the proportion of fish following the more attractive replica (i.e., an estimate of p_{nj}) and the proportion of trials in which all fish followed the more attractive replica (i.e., a_{nj}). In the experimental data, p_{nj} increases with group size (linear regression: $r^2 = 0.96$, $n = 4$, $p = 0.02$; Figure 2A). Indeed, p_{1j} is significantly different from one half in only four of the ten phenotype treatments (i.e., two-tailed sign test is significant at $p = 0.03$ if more than 13 out of 20 fish prefer one of the two replicas), whereas p_{2j} , p_{4j} , and p_{8j} are significantly different from one half in seven, nine, and ten of the treatments, respectively. a_{nj} remains constant or decreases slightly with group size (linear regression: $r^2 = 0.92$, $n = 4$, $p = 0.041$; Figure 2B).

The increase in p_{nj} confirms that as group size increases, individuals converge increasingly on the attractive replica option, suggesting that the fish make consensus decisions. The slight decrease in a_{nj} suggests, however, that consensus is not as accurate as that predicted by Condorcet’s theorem. In some cases, a small number of individuals do not follow the consensus. In other cases, the group as a whole reaches near consensus to follow the less attractive replica.

following a particular replica is independent of the number of fish; i.e., $p_{nj} = p_{1j}$. Furthermore, we expect the number of trials in which all individuals follow the most attractive replica to decrease exponentially with group size; i.e., $a_{nj} = p_{1j}^n$.

Aggregated Decision

The group remains aggregated under all circumstances but individuals do not exchange information. Under this hypothesis, in any given trial, all individuals follow the same replica, and the expected proportion of times that a particular replica is chosen by the group is independent of group size; i.e., $p_{nj} = p_{1j}$ and $a_{nj} = p_{1j}$.

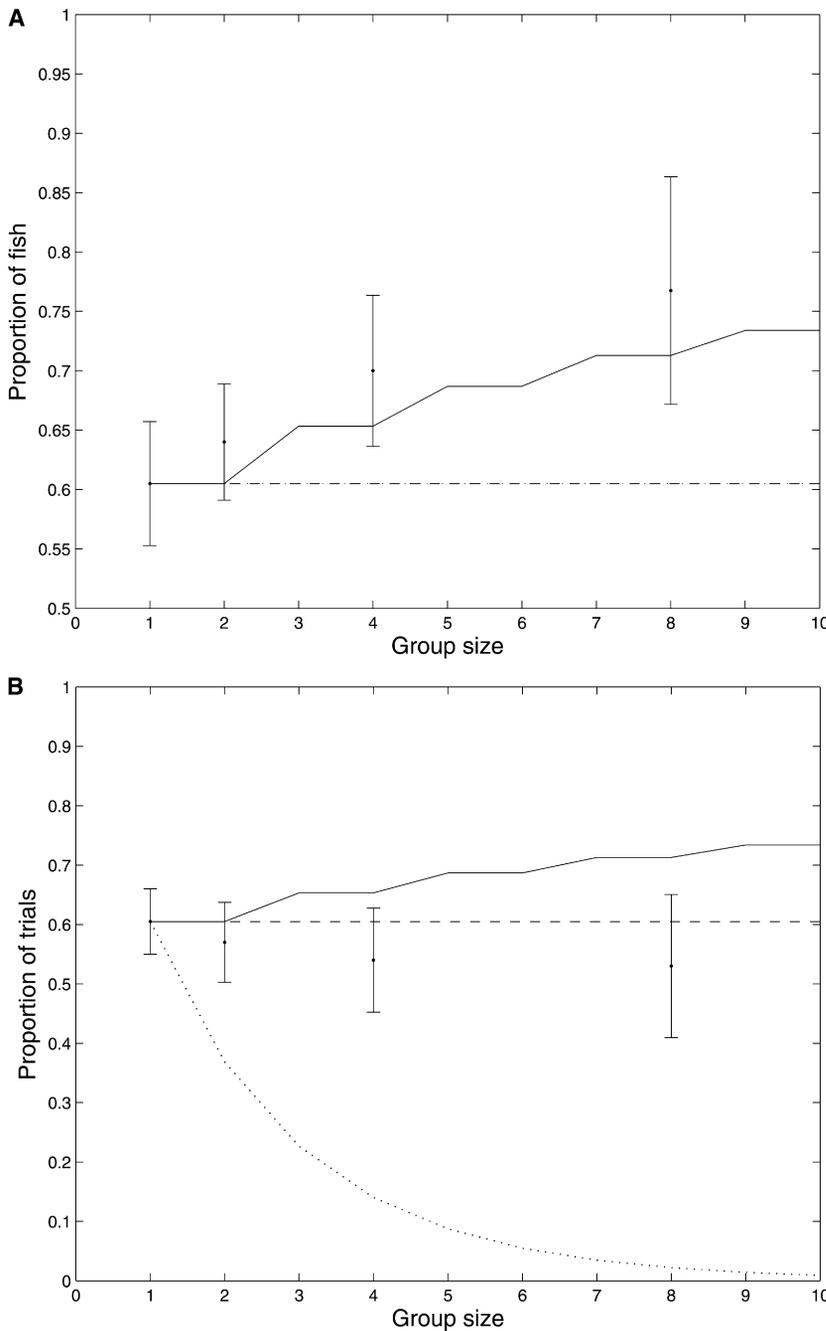


Figure 2. Proportions of Fish Following the More Attractive Leader and Trials in which All Fish Followed the More Attractive Leader

Hypothesized models for independent (dotted line), aggregate (dashed line), and consensus (solid line) decisions with the average (dots) and standard deviation (error bars) across all experimental treatments are shown.

(A) Proportions of fish following the more attractive leader over all trials. Note that the independent and aggregate models make the same prediction and the lines overlap.

(B) Trials in which all fish followed the more attractive leader.

In previous experimental work on leadership by identical conspecific replicas, i.e., those with no phenotypic differences, we established a simple quorum-response model for decision making [19]. Each individual has a probability, per time step, of going left of

$$a + (m - a) \times \frac{(L(t) - L(t - T))^k}{U(t)^k + (L(t) - L(t - T))^k + (R(t) - R(t - T))^k} \quad (1)$$

in which a is the probability per time step of spontaneously making a decision to go left, m is the maximum probability of making a decision, and k is the steepness of the fish response to conspecifics. $U(t)$ is the number of uncommitted individuals at time t ; and $L(t)$ and $R(t)$ are, respectively, the total number of individuals that have gone left and right by time t . In this earlier work, we fit the model parameters T , a , and m .

In order to apply our earlier model to the current data set, we need to incorporate the bias introduced by differences in the phenotypes of the replicas. There are two alternative hypotheses that could be used in incorporating the bias to the most attractive replica, both of which produce the same results for single-fish trials. One hypothesis is that each fish has a greater

Independent, aggregated, and Condorcet decisions are idealizations of the experimental outcomes, and these hypotheses make no predictions about how consensus is achieved. In particular, these idealizations do not describe the mechanisms through which a decision is reached. Recent research has established that quorum responses, in which an animal's probability of committing to a particular option increases sharply when a threshold number of other individuals have committed to it, are an important mechanism in the decision making of ants [15–17], honey bees [18], cockroaches [14], fish [19], and even humans [20]. Mathematical models predict that quorum responses may avoid some of the limitations of other types of copying behavior because information cascades do not begin until after a threshold number of independent individuals have demonstrated their preference [21].

tendency to follow the more attractive replica. In the model, we set the probability of spontaneously following the more attractive replica to be $ap_{1j}/(1 - p_{1j})$, whereas the corresponding parameter for the less attractive replica remains a . Previously, we showed that such a simulation does produce the increase in the proportion following the more attractive replica as the group size increases [19]. However, rerunning these simulations for the values of p_{1j} measured in our current experiments does not produce a quantitative fit to the data. Instead, it consistently underestimates the number of fish following the more attractive replica.

An alternative hypothesis is that with some small probability, a fish can detect a difference between the images and follow the more attractive of the two. In this case, the fish that detect the difference ignore the other fish and immediately move

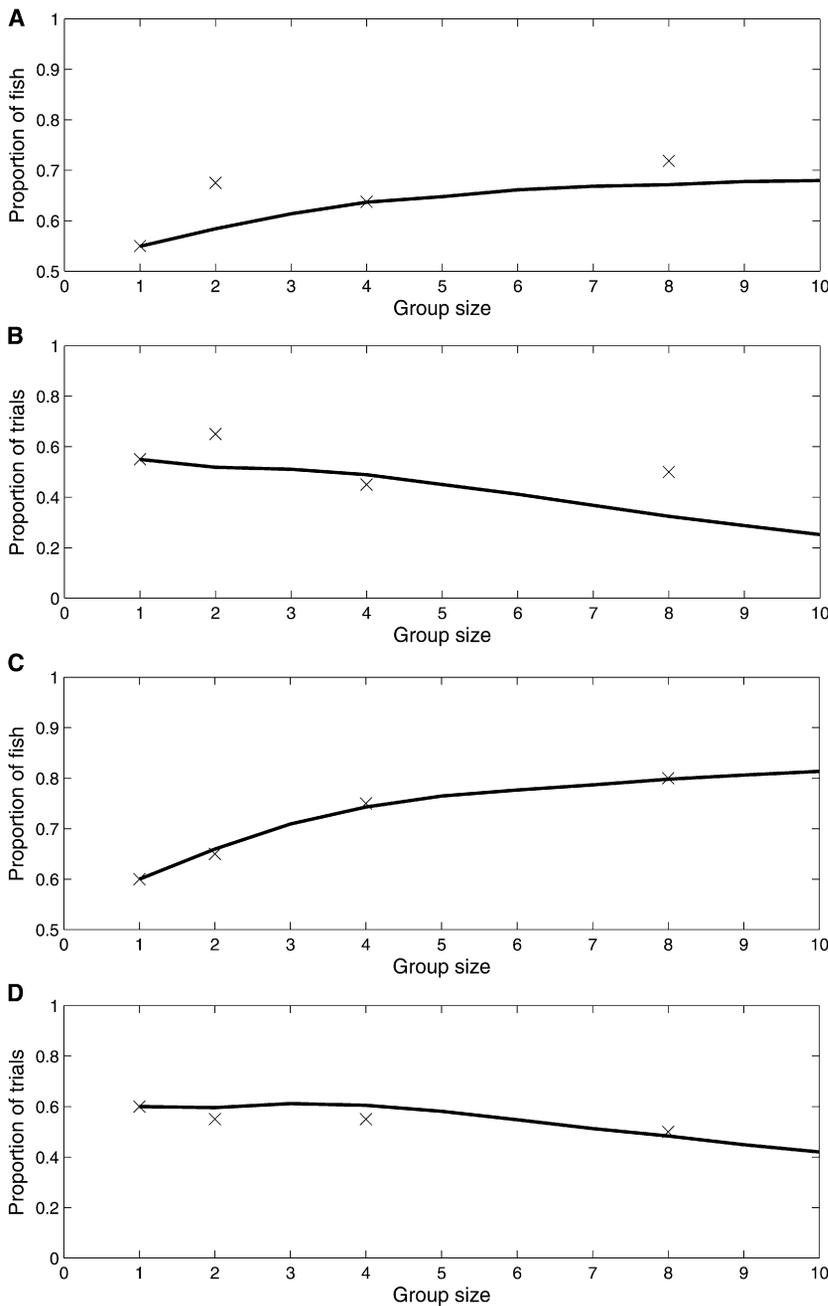


Figure 3. The Proportion of Fish Making the “Correct” Choice and the Proportion of Trials in which All Fish Make the Correct Choice, Comparisons to the Quorum-Response Model

The proportion fish making the “correct” choice (A and C) and the proportion of trials in which all fish make the correct choice (B and D) for the data compared to the average of 100,000 simulations of the quorum-response model for large-versus-medium (A and B) and dark-versus-light (C and D) treatments. See Figure S2 for the same figures for all other experimental treatments.

toward the more attractive replica. The remaining fish use the above quorum-response rule to make their decision. To model this hypothesis, we set this bias as a probability of $p_{bias} = 2p_{1j} - 1$, in which p_{1j} for each treatment is measured from single-fish experiments only, that a fish ignores the other fish and immediately moves toward the more attractive replica. We then set $R(0) = 1+X$, $U(0) = n-X$, and $L(0) = 1$, in which n is the group size and X is a binomially distributed random variable with parameters p_{bias} and n . For this latter hypothesis, we simulated the model for groups of $n = 1-10$ fish for each of the ten different treatments. Figure 3 shows how the model compares to the data in two treatments, large versus medium and dark versus light. This model quantitatively reproduced both the increase in the proportion of fish following the more attractive replica as the group size increases and the slightly decreasing proportion of trials in which all fish follow this

replica. The model also reproduced the distribution over all trials of the number of fish following the more attractive replica (see Figure S2). Similar results were seen when the quorum-response model was compared to other treatments: the model reproduced the same pattern of improvement in decision making with increase in group size as that seen in the data, for all treatments but the medium versus light treatment (see Figure S3).

The quorum-response rule provides a simple and effective way of integrating information. Individuals watch the decisions of others before committing themselves to a decision. In the model, one or two individuals sometimes take the less attractive option initially, but usually a larger number of individuals have taken the more attractive option. Undecided individuals are biased toward also taking the option that is more popular, and this choice becomes amplified. The data are consistent with this rule. For larger group sizes, nearly all the fish take the same, usually more attractive but sometimes less attractive, option. These consensus decisions are achieved by waiting until a threshold number of fish have made a particular decision. The threshold increases with group size, and thus so, too, does the accuracy of decision.

Our results support the hypothesis that relatively naive copying behavior can be an effective strategy for consensus decision making [21, 22]. In the study of animals, and particularly in the study of humans, information cascades for “suboptimal” choices are provided as evidence that naive copying can be a poor behavioral strategy. For example, economic bubbles and fashion trends are attributed to lack of independence between the individuals involved in these activities [23, 24]. Similarly, observations of humans [25–27] and other animals [12, 28] surrendering their own personal information in order to conform socially could be viewed as resulting from a cost of disobedience. Our results show, rather, that submission to peers and occasional suboptimal cascades can be explained simply as a byproduct of what is usually accurate, consensus decision making. Although the fish do not achieve the upper bound for accuracy predicted by Condorcet’s theorem, they are highly effective in integrating information without direct comparison of the available options.

Experimental Procedures

We presented groups of three-spined sticklebacks (*Gasterosteus aculeatus*; a common freshwater fish) with images of conspecifics. The groups of sticklebacks were added to a transparent Perspex box in an experimental arena that offered a choice of two identical refugia, both equidistant from their starting point. Fish could then be guided from this starting point toward the refugia by remote-controlled mounted images of conspecifics. We created the images by taking a digital image of a stickleback, printing this out onto transparent film, and mounting it onto microscope slides with clear tape. Each slide was fitted with a pair of small hooks so that it could be attached to a guide line of fine monofilament line. Finally, each slide was attached to an additional piece of monofilament line, which was attached to an electric motor that could then tow the slide along the guide line at a fixed speed. Sticklebacks responded to replicas presented in this way by approaching them and, as the slides moved, by following them. Controls of blank slides or of images of heterospecifics (minnows [*Phoxinus phoxinus*]) failed to elicit a consistent following response. In total, we produced 11 different slide-mounted conspecific images from the original image by manipulating its appearance using Adobe Photoshop. We created the 11 different images by varying one biologically meaningful characteristic in each case: we varied body length to produce small (25 mm length), medium (35 mm), and large (45 mm) images; we varied abdomen profile to produce fat (convex profile), medium (straight profile), and thin (concave profile) images; we varied contrast to produce light, medium, and dark images; and finally, we added small black spots to one image and not to its counterpart image. In each case, we produced two versions, facing opposing directions, so that each image could be presented on either the left or the right side of the experimental arena.

The images were attached to one of two guide lines extending from one end of the arena, positioned near the Perspex box containing the sticklebacks (termed “focal fish”), to each refuge. In each trial, we presented the focal fish with a choice between two such replicas. First, we acclimatized the fish for 5 min within the Perspex box before it was lifted, freeing the focal fish. Simultaneously, a motor started to tow the images, at a speed of one body length per s, to the far end of the arena. The experiments continued until all fish had entered the shaded goal zones or refuges (see Figure S1). These refuges are preferred by the fish even in the absence of a replica fish. The side at which the images were presented was randomized to eliminate potential bias. In the vast majority of experiments, the fish followed to the goal area, but in a few cases, a single “errant” fish remained motionless. If after 100 s this fish had not reached a goal, the trial was repeated and these results discarded. For each phenotype treatment and each group size, we conducted 20 trials. In each phenotype treatment, the image that was followed most often in the single-fish trials was assigned to be the more attractive replica. Although these single-fish trials did not always yield a significant preference for the replica within each treatment (see “Condorcet” Decision in Results and Discussion), our assignment both preserved a transitive relationship between comparable phenotypes (i.e., large versus medium versus small; fat versus medium versus thin; dark versus medium versus light) and was consistent with the significant preferences seen in experiments on larger numbers of fish.

Supplemental Data

Supplemental Data include three figures and can be found with this article online at [http://www.current-biology.com/S0960-9822\(08\)01422-X](http://www.current-biology.com/S0960-9822(08)01422-X).

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