

Corrections

APPLIED PHYSICAL SCIENCES, BIOPHYSICS AND COMPUTATIONAL BIOLOGY

Correction for “Cancer radiotherapy based on femtosecond IR laser-beam filamentation yielding ultra-high dose rates and zero entrance dose,” by Ridthee Meesat, Hakim Belmouaddine, Jean-François Allard, Catherine Tanguay-Renaud, Rosalie Lemay, Tiberius Brastaviceanu, Luc Tremblay, Benoit Paquette, J. Richard Wagner, Jean-Paul Jay-Gerin, Martin Lepage, Michael A. Huels, and Daniel Houde, which appeared in issue 38, September 18, 2012, of *Proc Natl Acad Sci USA* (109:E2508–E2513; first published August 27, 2012; 10.1073/pnas.1116286109).

The authors note that they omitted a reference to an article by Dumont et al. The complete reference appears below.

Also, on page E2512, right column, third full paragraph, lines 1–3 “pGEM-3Zf(-) plasmid DNA (3,197 bp, Promega) was extracted from *Escherichia coli* DH5 α and purified with the QIAfilter Plasmid Giga Kit (Qiagen)” should instead appear as “pGEM-3Zf(-) plasmid DNA (3,197 bp, Promega) was prepared in the laboratory of Dr. Darel Hunting. The plasmid was amplified and extracted from *Escherichia coli* JM109 and purified with the QIAfilter Plasmid Giga Kit (Qiagen) followed by removal of tris-EDTA buffer using homemade Sephadex G50 (Pharmacia) columns, according to the method published by Dumont et al. (56).”

Lastly, the following statement should be added to the Acknowledgments: “The authors wish to thank Dr. Darel Hunting for providing the plasmid DNA used in this work.”

56. Dumont A, Zheng Y, Hunting D, Sanche L (2010) Protection by organic ions against DNA damage induced by low energy electrons. *J Chem Phys* 132(4):045102.

www.pnas.org/cgi/doi/10.1073/pnas.1301033110

ECOLOGY

Correction for “A common rule for decision making in animal collectives across species,” by Sara Arganda, Alfonso Pérez-Escudero, and Gonzalo G. de Polavieja, which appeared in issue 50, December 11, 2012, of *Proc Natl Acad Sci USA* (109:20508–20513; first published November 28, 2012; 10.1073/pnas.1210664109).

The authors note that on page 20509, left column, first full paragraph, line 15, “ $\alpha = (\log(a) + \log(1/0.95 - 1))/\log(s)$ ” should instead appear as “ $\alpha = (\log(a) - \log(1/0.95 - 1))/\log(s)$ ”. This typographical error does not affect the calculations or conclusions of the article.

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APPLIED BIOLOGICAL SCIENCES

Correction for “pHLIP peptide targets nanogold particles to tumors,” by Lan Yao, Jennifer Danniels, Anna Moshnikova, Sergey Kuznetsov, Aftab Ahmed, Donald M. Engelman, Yana K. Reshetnyak, and Oleg A. Andreev, which appeared in issue 2, January 8, 2013, of *Proc Natl Acad Sci USA* (110:465–470; first published December 24, 2012; 10.1073/pnas.1219665110).

The authors note that the author name Jennifer Danniels should instead appear as Jennifer Daniels. The corrected author line appears below. The online version has been corrected.

Lan Yao, Jennifer Daniels, Anna Moshnikova, Sergey Kuznetsov, Aftab Ahmed, Donald M. Engelman, Yana K. Reshetnyak, and Oleg A. Andreev

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PHARMACOLOGY

Correction for “Local injection of dsRNA targeting calcitonin receptor-like receptor (CLR) ameliorates *Clostridium difficile* toxin A-induced ileitis,” by Aditi Bhargava, Matthew S. Clifton, Pallavi Mhsake, Min Liao, Charalabos Pothoulakis, Susan E. Leeman, and Eileen F. Grady, which appeared in issue 2, January 8, 2013, of *Proc Natl Acad Sci USA* (110:731–736; first published December 24, 2012; 10.1073/pnas.1219733110).

The authors note that the author name Pallavi Mhsake should instead appear as Pallavi Mhaske. The corrected author line appears below. The online version has been corrected.

Aditi Bhargava, Matthew S. Clifton, Pallavi Mhaske, Min Liao, Charalabos Pothoulakis, Susan E. Leeman, and Eileen F. Grady

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A common rule for decision making in animal collectives across species

Sara Arganda^{1,2}, Alfonso Pérez-Escudero², and Gonzalo G. de Polavieja³

Instituto Cajal, Consejo Superior de Investigaciones Científicas, 28002 Madrid, Spain

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A diversity of decision-making systems has been observed in animal collectives. In some species, choices depend on the differences of the numbers of animals that have chosen each of the available options, whereas in other species on the relative differences (a behavior known as Weber's law), or follow more complex rules. We here show that this diversity of decision systems corresponds to a single rule of decision making in collectives. We first obtained a decision rule based on Bayesian estimation that uses the information provided by the behaviors of the other individuals to improve the estimation of the structure of the world. We then tested this rule in decision experiments using zebrafish (*Danio rerio*), and in existing rich datasets of argentine ants (*Linepithema humile*) and sticklebacks (*Gasterosteus aculeatus*), showing that a unified model across species can quantitatively explain the diversity of decision systems. Further, these results show that the different counting systems used by animals, including humans, can emerge from the common principle of using social information to make good decisions.

collective behavior | public information | probability matching

Sensory data always has some degree of ambiguity, so animals need to make decisions by estimating the properties of the environment from uncertain sensory data (1–5). This estimation has been shown to be close to optimal in many cases, making optimal Bayesian decision making a successful framework shared by behavioral, neurobiological, and psychological studies (1–7).

A richer scenario for decision making takes place when animals move in groups. In this case, the behaviors of other animals are an extra source of information (6–34). Animals of different species have been observed to incorporate this extra information in their decisions in different ways. Some species make decisions that can be explained using the differences of the numbers of animals taking each option (21, 22), others according to the relative differences (Weber's law) (23, 24) or using other rules (25–34). This diversity of decision schemes has translated into a diversity of models (21, 22, 24–34).

To search for a unified framework having the diversity of decision-making schemes as particular cases, we generalized Bayesian decision making to the case of animal collectives. Our previous attempt at building such a theory predicted that the only relevant social information is the difference of the numbers of individuals already choosing each available option, and not the numbers themselves or the relative differences (or Weber's law) (22). However, this theory was limited to the particular case in which only one of the options could be a good option (22). We have now generalized the theory, allowing all available options to be good or bad options. We found that this generalization explains the diversity of decision rules observed in collectives, maintaining the same conceptual and mathematical simplicity, and containing our previous theory as a particular case. We have tested the theory experimentally in decision experiments using zebrafish (*Danio rerio*), but to cover the diversity of decision systems, we have also tested it using rich datasets of decision making in argentine ants (*Linepithema humile*) (24) and three-spined sticklebacks (*Gasterosteus aculeatus*) (25, 26). We found a quantitative match between the theory and the different decision systems of these representative species.

Results

We studied how the behaviors of others should be taken into account to improve the estimations of the structure of the world and make decisions in animal collectives. For a situation with two identical options to choose from (Fig. 1A), we looked for the probability that one option, say x , is a good option given that n_x and n_y animals have already chosen options x and y , respectively. We used Bayesian theory to find an approximated analytic expression for this probability as (SI Text)

$$P(x \text{ is good}) = \frac{1}{1 + as^{-(n_x - kn_y)}} \quad [1]$$

Parameter a measures the quality of nonsocial information available to the deciding individual, and s measures how reliably an individual that has chosen x indicates to the deciding individual that x is a good option. According to Eq. 1, the higher the number of individuals that chose option x , n_x , the higher the probability that option x is good for the deciding individual, and more so the higher the reliability s of the information from the individuals that already chose x . However, each individual that chooses y decreases the probability that x is a good option. Parameter k measures the relative impact of these two opposing effects. Individuals need to decide based on the estimated probabilities in Eq. 1. A common decision rule in animals, from insects to humans, is probability matching, according to which the probability of choosing a behavior is proportional to the estimated probability (35–44),

$$P_x = \frac{P(x \text{ is good})}{P(x \text{ is good}) + P(y \text{ is good})} \quad [2]$$

This rule is known to be optimal when there is competition for resources (39, 40) and when the estimated probabilities change in time (41–44). Probability matching in Eq. 2, together with the estimation in Eq. 1, gives that the probability of choosing x is

$$P_x = \left(1 + \frac{1 + as^{-(n_x - kn_y)}}{1 + as^{-(n_y - kn_x)}} \right)^{-1}, \quad [3]$$

and $P_y = 1 - P_x$ is the probability of choosing y . The main implications of Eq. 3 are apparent in its plot (Fig. 1B). First, decision making in collectives is predicted to be different for low and high numbers of individuals. For low numbers, there is a fast

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¹Present address: Centre de Recherches sur la Cognition Animale, Centre National de la Recherche Scientifique Unité Mixte de Recherche 5169, Université Paul Sabatier, 31062, Toulouse, France.

²S.A. and A.P.-E. contributed equally to this work.

³To whom correspondence should be addressed. E-mail: gonzalo.polavieja@cajal.csic.es.

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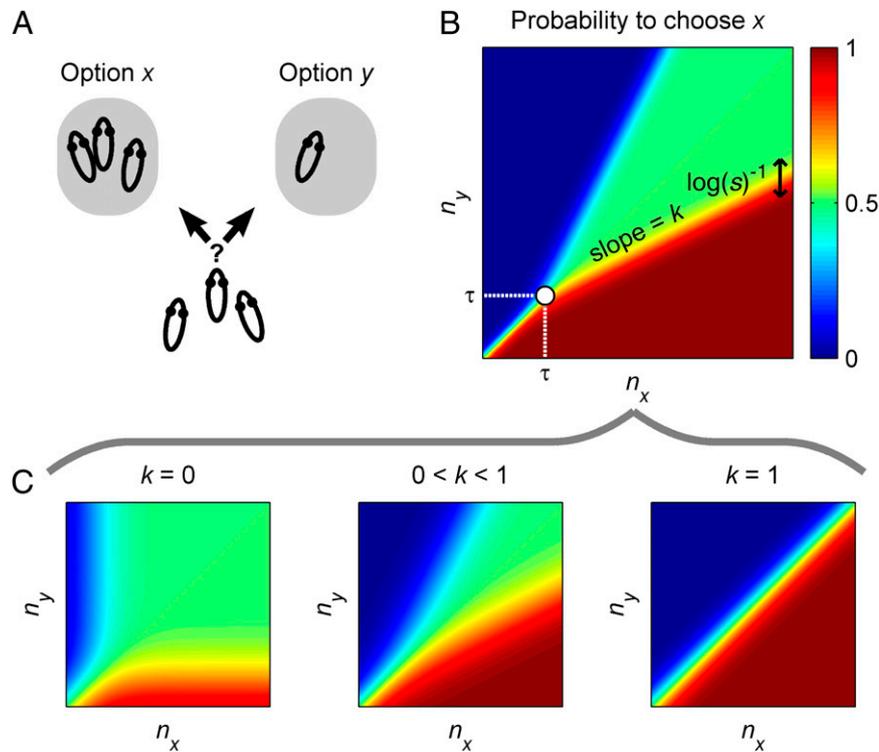


Fig. 1. A general decision-making rule in animal collectives. (A) Decision making between two sites when n_x and n_y animals have already chosen sites x and y , respectively. (B) The probability of choosing x in the general rule (Eq. 3), plotted as a function of the animals that have already chosen between the two sites, n_x and n_y . The theory predicts very different structure in the probability for the case of low and high numbers of animals, separated by point $\tau = \log(a)/(\log(s)(1-k))$. The rate of change of P_x in the transition regions depends on the reliability parameter s , with the width of these regions proportional to $1/\log(s)$. (C) Same as B but for three different values of parameter k : $k = 0$ (Left), $0 < k < 1$ (Center), and $k = 1$ (Right).

transition between preferring one side over the other, whereas for high numbers the transition has an intermediate region with no preference in which the probability has a plateau of value of one-half. There is a clear separation between the low- and high-numbers regimes at the point $\tau = \log(a)/(\log(s)(1-k))$ in which the plateau starts (Fig. 1B; *SI Text*). Second, in the high-numbers regime, the isoprobability curves are straight lines of slope k . We can use this slope to classify three very different scenarios we found to correspond to different experimental datasets: $k = 0$, $0 < k < 1$, and $k = 1$ (Fig. 1C).

For $k = 0$, the animals at one option do not impact negatively on the estimated quality of the other option; this can take place, for example, when animals at one option do not seem to have information about the other option. An important prediction for this case is that for high numbers of animals there is a large plateau of probability one-half of choosing each of the two options (Fig. 1C, *Left*). To have a significantly higher probability of choosing one option, say x , it is then needed not only that $n_x > n_y$ but also to be outside of the large plateau, which means that very few animals have chosen the other option y , $n_y < \tau$. A second prediction is that there is a finite number of animals that need to be distinguished; to see this, consider that the probability that option x is a good one (Eq. 1) for $k = 0$ increases monotonically with n_x and converges to 1. The number of animals n_x needed to reach a high probability of 0.95 is given by $\alpha = (\log(a) + \log(1/0.95 - 1))/\log(s)$ (Fig. S1). Beyond α the probability changes very little, thus in practice it is not necessary to count beyond that number. For a wide range of parameters a and s , α has low values, corresponding to counting up to a low number of animals (Fig. S1).

We have found that wild-type zebrafish (*D. rerio*) in a two-choice setup used for tests of sociability (45, 46) make choices that quantitatively correspond to the predictions of the $k = 0$ case. The setup has three chambers separated by transparent walls;

a central chamber with the zebrafish we monitor, and two lateral chambers with different numbers of zebrafish acting as social stimuli (Fig. 2A; *Materials and Methods*). An interesting feature of this setup is that it measures the behavior of a single individual when presented with social stimuli, allowing a direct test of the individual decision rule in Eq. 3. Specifically, we measured the probability that the focal fish chooses each of the two options for a range of configurations (Fig. 2B; each dot is the mean of typically $n = 15$ animals). We found that these experimental results correspond to Eq. 3 for $a = 11.2$, $s = 5$, and $k = 0$ (Fig. 2B, blue surface) with a robust fit (Fig. S2). To make a more quantitative comparison between theory and experiment, we highlighted several lines on the theoretical surface, using different colors to indicate different numbers of fish at option y . Fig. 2C compares the probability values for these five lines with the experimental data, showing a close match. The model offers both a quantitative fit to data and a simple explanation of the experimental result. Fish do not choose directly according to the number of other fish, but to how these numbers indicate that a place is a good option, giving a rule of “counting up to 3.”

The close match between experimental data and the decision-making model supports that zebrafish behavior corresponds to probabilistic estimations about the quality of sites using social information. However, the processing steps made by the fish brain need not have a one-to-one correspondence with the computational steps in the theory. Instead, a likely option is that zebrafish use simple behavioral rules that approximate good estimations. We found mechanistic models with simple probabilistic attraction rules for individual fish that approximate well the decision-making model and the data (Figs. S3 and S4).

The second case we consider has parameter k in the range from 0 to 1. For this range, the estimation that x is a good option increases with how many animals have already chosen x and decreases,

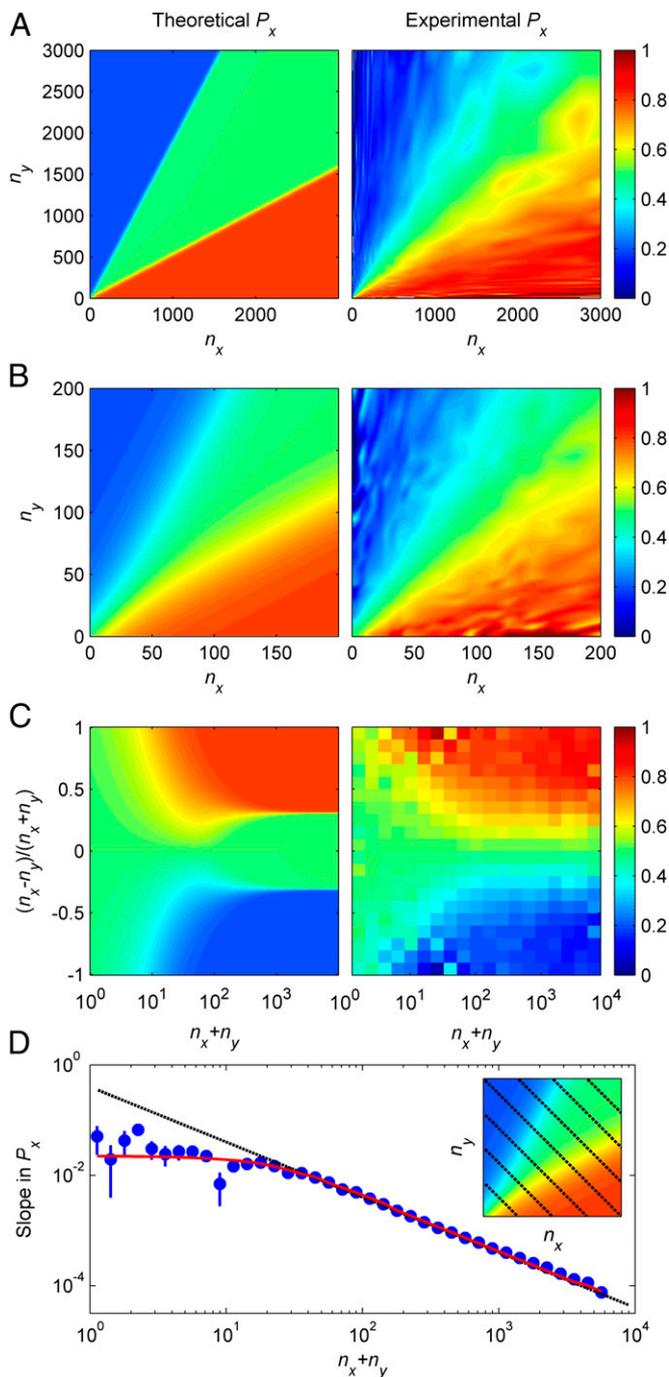


Fig. 3. Ant choices correspond to the general rule of decisions in collectives. (A) Probability of choosing option x as a function of how many ants have previously been at locations x and y , n_x and n_y , for theory (Left) using Eq. 4 with $a = 2.5$, $s = 1.07$, $k = 0.53$, $p_{\text{rand}} = 0.39$, and experiments (Right) from Perna et al. (24). (B) Detail of A. (C) Same as A but represented as a function of $\Delta N/N$ and N . (D) Slope of the probability of choosing x in A as obtained from a linear fit along the lines depicted in *Inset*. Experimental values (blue dots; error bars are 95% confidence interval), theory (red line), and Weber's law (black line).

have in common an effective ΔN rule for the experimental region (Fig. 4B), giving strong support to this rule in this dataset.

Discussion

Our results support that estimation by the brain using social information to counteract the ambiguity of sensory data is a fundamental principle in collective decision making. The theory explains

also the diversity in number discrimination schemes used in collective decisions, including counting up to a given number of animals, counting the difference of animals choosing among options, ΔN , or the relative difference, $\Delta N/N$, as well as observed deviations from these ideal cases and the existence of different counting regimes for high and low numbers as observed in many species, including humans (47, 48). A single mathematical rule contains all these cases and can be used as a first-principles approach to quantitatively study decisions in animal collectives.

One important ingredient of our theory is the use of probability matching (Eq. 2); for symmetric decisions, it implies a functional form of the type $P_x = f(x, y)/(f(x, y) + f(y, x))$. Our model in Eq. 3 is a particular case of this function, with $f(x, y)$ derived from an approximation to Bayesian estimation. Interestingly, many previous approaches derive from the form $P_x = f(x)/(f(x) + f(y))$ (21, 22, 27, 28), which is also a particular case of $P_x = f(x, y)/(f(x, y) + f(y, x))$, and therefore compatible with probability matching. In other cases, the basic form $P_x = f(x)/(f(x) + f(y))$ has been modified by adding constant terms (29, 30) or an extra function (25), as $P_x = f(x)/(f(x) + f(k))$, with k a constant when animals have access to a single choice (31, 32, 34). Weber behavior can also be seen as a particular case. It has been previously described using a function (24) that can be expressed as $f(x, y) = 1/2 + \delta(n_x - n_y)/(n_x + n_y)$, with δ between 0 and 1/2. This function obeys $f(x, y) + f(y, x) = 1$, so in this case $P_x = f(x, y)$, following Weber behavior.

These previous functions are very useful when applied to particular datasets because they may use few parameters in these conditions. In particular, our previous model (22), a particular case of Eq. 3 (SI Text), used only one parameter in the symmetric experiments with sticklebacks, and a model with two parameters described the ants dataset (24). However, these two models cannot fit the three datasets or even two of them (Fig. S9 A and D and S10). For the zebrafish data in Fig. 2, none of the previously proposed functions (21, 22, 24, 27–29) give a good fit of the plateau in the data (Fig. S9). Our approach has been developed to be applied in very different species and conditions, here tested for three large datasets in three different species. One important factor in this ability to describe different datasets is that our basic function $f(x, y)$ has a term $s^{-(n_x - k n_y)}$ that captures how the estimated quality of an option depends not only on the animals choosing that option but also on the animals choosing the other option. These two sources of information are balanced by parameter k , and different datasets are found to correspond to different balances k .

Previous functions describing ant foraging include a constant term that represents a threshold of pheromone concentration below which ants do not react (24, 27, 28). In this way, these functions can describe the deviation from Weber's law at low pheromone concentration (24). In our case, the theory naturally shows this behavior as one more particular case of the predicted difference between a low and high number of animals. Comparing the two approaches, it is interesting to consider that the behavior for low numbers that is predicted from estimation theory can be achieved in ants using a threshold of pheromone concentration.

An advantage of our approach is that the form of the function f is derived for any type of setup simply from estimation given non-social sensory data and the behaviors of others (SI Text). For example, we predict for a symmetric setup with N options a generalization of Eq. 1 of the form

$$P(x \text{ is good}) = \frac{1}{1 + a s^{-(n_x - k M)}}$$

with $M = \sum_{i \neq x}^N n_i$ the total number of animals choosing any option except x (see Eq. S10 for the more general case of asymmetric choices).

A further advantage is that the parameters a , s , and k are not only fitting parameters but have expressions, Eqs. S4, S9, and

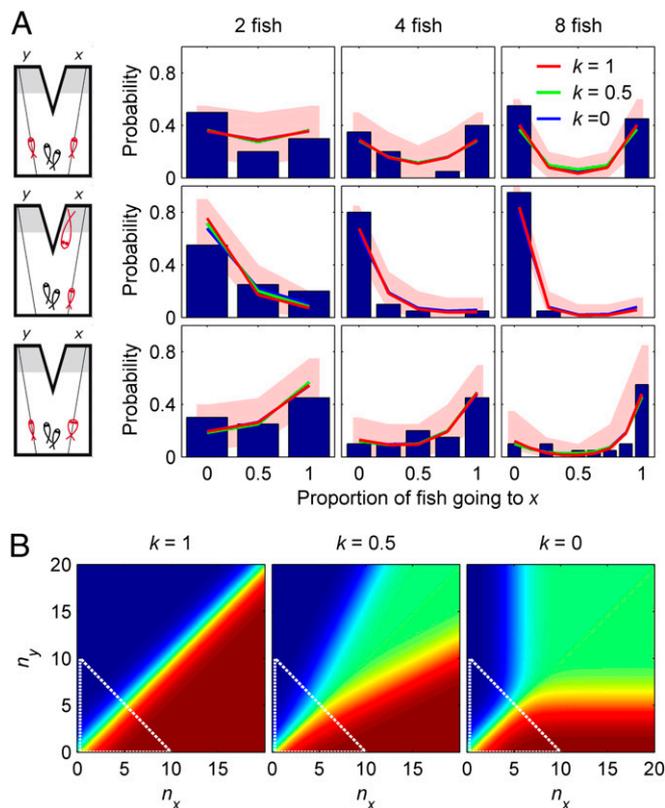


Fig. 4. Stickleback choices correspond to the general rule of decisions in collectives. (A) Probability of finding a final proportion of sticklebacks choosing option x (blue histograms are experimental results from refs. 25 and 26 and theoretical values as lines for $k = 1$, $k = 0.5$, and $k = 0$) for different group sizes (two, four, and eight fish) and for three types of setups: a symmetric setup with different numbers of replica fish going to x and y (Top), a setup with a replica predator at x and different replica fish going to x (Middle), and a symmetric setup with modified replica fish (Bottom). See model parameters and 68 additional experiments with fits in Fig. S7. (B) Theoretical P_x for $k = 1$, $a = 1$ (Left), $k = 0.5$, $a = 5$ (Center), and $k = 0$, $a = 224$ (Right), and $s = 2.5$ in the three cases. All models require an effective ΔN rule to compare with data for the number of animals used in experiments (triangle).

S16, respectively, which give additional predictions. For example, the social reliability parameter is given by

$$s = \frac{P(\beta|X, C)}{P(\beta|\bar{X}, C)}$$

with β a given animal behavior. This expression means that the social reliability parameter s is higher for a behavior β that is produced with high probability when x is a good option, and with very low probability when it is not a good option. Among all behaviors, those with higher s allow an individual to obtain a higher probability that option x is a good one (Eq. 1), so we expect them to have a larger effect on collective decision making.

Another advantage of an approach based on a theory of estimation is that generalizations of the theoretical expressions can be envisaged deriving models using fewer assumptions. For example, including dependencies in the behaviors of the other individuals and explicit space and time variables should be natural extensions of the theory.

Materials and Methods

Experimental Protocol for Zebrafish. All procedures met with European Economic Community (EEC) guidelines for animal experiments under Directive 86/609/EEC. Experimental procedures were approved by the Bioethics Sub-

committee of Consejo Superior de Investigaciones Científicas. We used wild-type adult zebrafish, *D. rerio*, of both sexes. Fish were acclimatized to the setup water for 1 d before the experiments (Fig. S11). At 1 h before the experiment, each fish was isolated and fed to ensure uniform nutritional status across individuals. A focal fish entered the setup and swam freely in a central chamber between two social chambers with different number of fish and separated from the choice chamber by glass. Once a fish had been recorded for 5 min it could be placed in one of the lateral chambers as a social stimulus for another fish. The fish in the lateral chambers were interchanged between trials to ensure uniformity, and sides were randomized. The central chamber of the setup was washed between trials to remove odor traces. We computed the probability P_x as the fraction of time the focal fish spent on the black region close to one of the social chambers, x . This fraction of time converges to P_x for a fish that makes repeated decisions choosing x (y) with probability P_x ($P_y = 1 - P_x$). A total of 238 fish were tested only once. To test the effect of previous experience, another 233 trials were performed with fish that were tested several times. We found no significant difference between the two groups in the mean times spent at each side (Fig. S12), so all data were pooled for Fig. 2.

Model with Noise Added to the Decision Rule. The model in Eq. 3 has a good agreement with data from experiments using the Argentine ant, *L. humile* (24), except that experimental probabilities do not reach values as close to 0 or 1 as the theory. To account for the experimental data, we made a simple modification of the model by assuming that the ant has some probability p_{rand} of making the decision at random motivated by unknown factors. Then, with probability $(1 - p_{\text{rand}})$, the ant makes the decision according to Eq. 3. Therefore, the probability of turning toward x is

$$P_x = \frac{p_{\text{rand}}}{2} + (1 - p_{\text{rand}}) \left(1 + \frac{1 + a s^{-(n_x - k n_y)}}{1 + a s^{-(n_y - k n_x)}} \right)^{-1}. \quad [4]$$

The parameters that best fit the ant data are $a = 2.5$, $s = 1.07$, $k = 0.53$, and $p_{\text{rand}} = 0.39$. This same model can be applied to the zebrafish and stickleback datasets, but in these cases the best fit is obtained for $p_{\text{rand}} \approx 0$, which corresponds to Eq. 3.

Analysis of the Ants Dataset. Both the raw dataset and preprocessing routines were provided by Perna et al. (24), and we used their data assuming no evaporation of pheromone (this assumption does not change the results significantly). We calculated from the data the probability of turning right or left, not a continuous angle, to compare directly to our predicted probabilities. To reduce the noise in the experimental maps of Fig. 3, we symmetrized the data so that the probability shown at point (n_x, n_y) is obtained as $(P_x(n_x, n_y) + (1 - P_x(n_y, n_x)))/2$.

Experimental data from Perna et al. (24) measures a quantity that is proportional to the number of ants previously at the left/right of the deciding ant, not directly the numbers, so the number of ants (n_x, n_y) used in the plots are related to the actual number of ants that count for the decision $(n_{x, \text{true}}, n_{y, \text{true}})$ by $n_x = \lambda n_{x, \text{true}}$, $n_y = \lambda n_{y, \text{true}}$, where λ is an unknown proportionality constant. This relation means that the model still applies but with $s = s_{\text{true}}^\lambda$, where s_{true} is the actual value of the reliability parameter.

Asymmetric models. For the case of sticklebacks deciding in the presence of a predator (Fig. 4A, Middle), we derived the more general asymmetric version of Eq. 1, Eq. S22 (Figs. S13 and S14). We also derived Eq. S23 for the case with two different types of replicas (Fig. 4A, Bottom).

Fitting Procedures. To fit the model's parameters to the data, we performed 2D exhaustive searches in the space of parameters. For functions with more than two parameters, we performed the search successively with all possible pairs of parameters. In these cases we repeated the fit several times starting from different initial conditions, always getting the same final result.

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