Collective Animal Behavior from Bayesian Estimation and Probability Matching

Alfonso Pérez-Escudero*, Gonzalo G. de Polavieja*

April 5, 2011

Nature Precedings : hdl:10101/npre.2011.5939.1 : Posted 5 May 2011

Abstract

Animals living in groups make movement decisions that depend, among other factors, on social interactions with other group members. Our present understanding of social rules in animal collectives is based on empirical fits to observations and we lack first-principles approaches that allow their derivation. Here we show that patterns of collective decisions can be derived from the basic ability of animals to make probabilistic estimations in the presence of uncertainty. We build a decision-making model with two stages: Bayesian estimation and probabilistic matching. In the first stage, each animal makes a Bayesian estimation of which behavior is best to perform taking into account personal information about the environment and social information collected by observing the behaviors of other animals. In the probability matching stage, each animal chooses a behavior with a probability given by the Bayesian estimation that this behavior is the most appropriate one. This model derives very simple rules of interaction in animal collectives that depend only on two types of reliability parameters, one that each animal assigns to the other animals and another given by the quality of the non-social information. We test our model by obtaining theoretically a rich set of observed collective patterns of decisions in three-spined sticklebacks, *Gasterosteus aculeatus*, a shoaling fish species. The quantitative link shown between probabilistic estimation and collective rules of behavior allows a better contact with other fields such as foraging, mate selection, neurobiology and psychology, and gives predictions for experimenst directly testing the relationship between estimation and collective behavior.

Introduction

Animals need to make decisions without certainty in which option is best. This uncertainty is due to the ambiguity of sensory data but also to limited processing capabilities, and is an intrinsic and general property of the representation that animals can build about the world. A general way to make decisions in uncertain situations is to make probabilistic estimations [1, 2]. There is evidence that animals use probabilistic estimations, for example in the early stages of sensory perception [3–11], sensory-motor transformations [12–14], learning [15–17] and behaviors in an ecological context such as strategies for food patch exploitation [18–20] and mate selection [21], among others [13, 17, 21, 22].

An additional source of information about the environment may come from the behavior of other animals (social information) [23–27]. This information can have different degrees of ambiguity. In particular cases, the behavior of conspecifics directly reveals environmental characteristics (for example, food encountered by another individual informs about the quality of a food patch). Cases in which social information correlates well with the environmental characteristic of interest have been very well studied [28–36]. But in most cases social information is ambiguous and potentially misleading [26, 37]. In spite of this ambiguity, there is evidence that, at least in specific cases such as predator avoidance [38, 39] and mate choice [40], animals use this kind of information.

Social animals have a continuous flow of information about the environment coming from the behaviours other animals. It is therefore possible that social animals use it at all times, making probabilistic estimations to counteract its ambiguity. If this is the case, social information might be a major determinant of the structure of animal collectives. In order to test this hypothesis, we have developed a Bayesian decision-making model that includes both personal and social information that naturally weights them according to

---

*Instituto Cajal, Consejo Superior de Investigaciones Científicas, Av. Doctor Arce, 37, 28002 Madrid, Spain. Department of Theoretical Physics and Instituto "Nicolás Cabrera" de Física de Materiales, Universidad Autónoma de Madrid, 28049 Madrid, Spain. E-mail: alfonso.perez.escudero@cajal.csic.es, gonzalo.polavieja@cajal.csic.es

their reliability in order to get a better estimate of the environment. All members of the group can then use these improved estimations to make better decisions, and collective patterns of decisions then emerge from these individuals interacting through their perceptual systems.

We show that this model derives social rules that economically explain detailed experiments of decision-making in animal groups [41,42]. This approach should complement the empirical approach used in the study of animal groups [41–45], finding which mathematical functions should correspond to each experimental problem and to propose experiments relating estimation and collective motion. The Bayesian structure of our model also builds a bridge between the field of collective behavior and other fields of animal behavior, such as optimal foraging theory [18–22] and others [21, 22]. Further, it explicitly includes in a natural way different cognitives abilities, making more direct contact with neurobiology and psychology [3–10, 17].

Results

General model

We derived a model in which each individual decides from an estimation of which behavior is best to perform. These behaviors can be to go to one of several different places, to choose among some behaviors like forage, explore or run away, or any other set of options. The general derivation of the model for any set of options can be found in the *Supporting Text*. For clarity, here we particularize to the case of choosing the best of two spatial locations, x and y. 'Best' may correspond to the safest, the one with highest food density or most interesting for any other reasons. We assume that each decision maker uses in the estimation of the best location both non-social and social information. Non-social information may include sensory information about the environment (i.e. shelter properties, potential predators, food items), memory of previous experiences and internal states. Social information consists of the behaviors performed by other decision-makers. Each individual estimates the probability that each location, say y, is the best one, using its non-social information (c) and the behavior of the other individuals (B),

$$P(Y|c, B), \tag{1}$$

where Y stands for 'y is the best location'. $P(X|c, B) = 1 - P(Y|c, B)$, because there are only two locations to choose from. We can compute the probability in Eq. **1** using Bayes' theorem,

$$P(Y|c, B) = \frac{P(B|Y, c)P(Y|c)}{P(B|X, c)P(X|c) + P(B|Y, c)P(Y|c)}. \tag{2}$$

Simply by dividing numerator and denominator by the numerator we find an interesting structure,

$$P(Y|c, B) = \frac{1}{1 + a\,S}, \tag{3}$$

where

$$a = \frac{P(X|c)}{P(Y|c)} \tag{4}$$

contains only non-social information, and

$$S = \frac{P(B|X, c)}{P(B|Y, c)} \tag{5}$$

captures all the social information. Non-social information (c) is also present in the social term S, so the same behavior can have differents effect on the estimation depending on the sensory information from the environment. Note that the simple multiplicative interaction between the social and non-social terms in Eq. **3** stems from Bayesian estimation, not requiring any approximations. In order to get an expression that depends on the individual behaviors observed by the deciding individual, we approximated S in Eq. **5** in the following way. The probability $P(B|Y, c)$ may be approximated using the assumption that the focal individual does not make use of the correlations among the behaviour of others, but instead assumes their behaviours to be independent of each other. Then, the probability of a given set of behaviors is just the product of the probabilities of the individual behaviors,

$$P(B|Y, c) = Z \prod_{i=1}^{N} P(b_i|Y, c), \tag{6}$$

where B is the set of all the behaviors of the other N animals, $B = \{b_i\}_{i=1}^{N}$, and b_i denotes the behavior of one of them, individual i. Z is a combinatorial term counting the number of possible decision sequences that lead to the set of behaviors B, that will cancel out in the next step. Substituing Eq. **6** and the corresponding expression for $P(B|X, c)$ into Eq. **5**, we get

$$S = \prod_{i=1}^{N} \frac{P(b_i|X, c)}{P(b_i|Y, c)}. \tag{7}$$

Instead of an expression in terms of as many behaviors as individuals, it may be more useful to consider a discrete set of behavioral classes. For example, in our two-choice example, these behavioral classes may be 'go to x' (denoted β_x), 'go to y' (β_y) and 'remain undecided' (β_u). Frequently these behavioral classes (or simply 'behaviors') will be directly related to the choices, so that each behavior will consist of choosing one option. For example, behaviors β_x and β_y are directly related to choices x and y, respectively. But there may be behaviors not related to any option as the case of undecision, β_u, or related to choices in an indirect way. Let us consider K different behavioral classes, $\{\beta_k\}_{k=1}^K$. We do not here consider individual differences for animals performing the same behavior (say, behavior β_1), so they have the same probabilities $P(\beta_1|X,c)$ and $P(\beta_1|Y,c)$. Thus, if for example the n_1 first individuals are performing behavior β_1, we have that $\prod_{i=1}^{n_1} \frac{P(b_i|X,c)}{P(b_i|Y,c)} = \left(\frac{P(\beta_1|X,c)}{P(\beta_1|Y,c)}\right)^{n_1}$. We can then write Eq. **7** as

$$S = \prod_{k=1}^{K} s_k^{n_k}, \tag{8}$$

where n_k is the number of individuals performing behavior β_k, and

$$s_k = \frac{P(\beta_k|X,c)}{P(\beta_k|Y,c)}. \tag{9}$$

The term s_k is the probability that an individual performs behavior β_k when x is the best option, over the probability that it performs the same behavior when y is the best choice. The higher s_k the more reliably behavior β_k indicates that x is better than y, so we can understand s_k as the reliability parameter of behavior β_k. If $s_k = \infty$ observing behavior β_k indicates with complete certainty that x is the best option, while for $s_k = 1$ behavior β_k gives no information. For $s_k < 1$ observing behavior β_k favors y as the best option, and more so the closer it is to 0. Note that $P(\beta_k|X,c)$ and $P(\beta_k|Y,c)$ are not the actual probabilities of performing behavior β_k, but estimates of these probabilities that the deciding animal uses to assess the reliability of the other decision-makers. These estimates may be 'hard-wired' as a result of evolutionary adaptation, but may also be subject to change due to learning.

We have so far only considered the perceptual stage of decision-making, in which the deciding individual estimates the probabilitiy for each behavior to be the best one. Now it must decide according to this estimation. A deterministic decision rule could be to go to y when $P(Y|c,B) > P(X|c,B)$. We however found a better correspondence with data using a softer version of this rule known as probability matching that has been found to apply in cognitive [46] and perceptual tasks [47]. According to this rule, the probability of going to y, P_y, is the same as the estimated probability that y is the best location, so

$$P_y = P(Y|c,B). \tag{10}$$

Alternatively, we could consider noisy versions of the deterministic rule but at the price of adding at least one extra parameter.

To summarize, using Eqs. 3, 8 and 10 we have that the probability that the deciding individual goes to y is

$$P_y = \left(1 + a \prod_{k=1}^{K} s_k^{n_k}\right)^{-1}. \tag{11}$$

In the following sections, we particularize Eq. **11** to different experimental settings to test its results against existing rich experimental data sets that have previously been fitted to different mathematical expressions [41, 42].

Symmetric set-up

We first considered the simple case of two identical equidistant sites, x and y, Fig. 1A, and the three behaviors 'go to x' (β_x), 'go to y' (β_y) and 'remain undecided' (β_u). Eq. **11** in this case reduces to

$$P_y = \left(1 + a\, s_x^{n_x} s_y^{n_y} s_u^{N-n_x-n_y}\right)^{-1}, \tag{12}$$

where n_x and n_y are the number of individuals that have already chosen x and y, respectively, and $N+1$ is the size of the group containing our focal individual and other N animals. As the set-up is symmetric, the sensory information available to the deciding individual is the same for both options so $P(X|c) = P(Y|c)$, and $a = 1$ according to Eq. **4**. Therefore, the non-social term in Eq. **12** cancels out. Also, since undecision is not related to any particular choice, symmetry imposes $P(\beta_u|X,c) = P(\beta_u|Y,c)$, so undecision is not informative, $s_u = 1$ (Eq. **9**). For the other two behaviors, going to x (β_x) and going to y (β_y), Eq. **9** gives

$$\begin{aligned} s_x &= \frac{P(\beta_x|X,c)}{P(\beta_x|Y,c)} \\ s_y &= \frac{P(\beta_y|X,c)}{P(\beta_y|Y,c)}. \end{aligned} \tag{13}$$

$P(\beta_x|X,c)$ and $P(\beta_y|Y,c)$ are the estimated probabilities of making the right choice, that is, going to x when x is the best option, or going to y when y is the best option. Since in this case the sensory information is identical for both choices the probability of making the correct choice must be the same for both options, $P(\beta_x|X,c) = P(\beta_y|Y,c)$. An analogous argument holds for the incorrect choices, $P(\beta_x|Y,c) = P(\beta_y|X,c)$, giving

$$s_x = 1/s_y. \tag{14}$$

In cases in which $s_x = 1/s_y$, we find it convenient to express reliability more generally as

$$s \equiv s_x = 1/s_y, \tag{15}$$

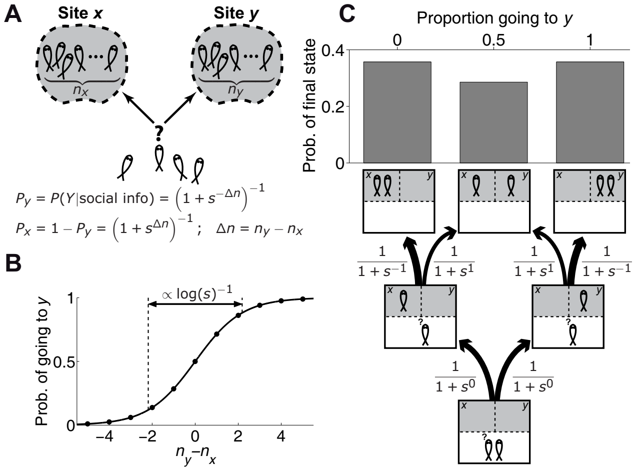

Figure 1. Model with individuals estimating which of two identical places is best. (*A*) Schematic diagram of individuals choosing between two identical locations x and y when there are already n_x (n_y) individuals at x (y). (*B*) Probability of going to y as a function of the difference between the number of individuals at y and x, Eq. **16**. (*C*) Sequential application of the behavioural rule in Eq. **16** with $s = 2.5$, for the simple case of a group of two individuals (bottom). The width of the arrows is proportional to the probability of each transition. The 3 possible final configurations, with different proportion of individuals going to y (0, 0.5 and 1), have different probabilities of taking place, with both fish together at x or y being more probable than a group split (top).

which is the ratio of the probability of making the correct choice and the probability of making a mistake, for both behaviors. Using this definition and given that $a = a_u = 1$, Eq. **12** reduces to

$$P_y = \left(1 + s^{-\Delta n}\right)^{-1}, \tag{16}$$

with the variable $\Delta n \equiv n_y - n_x$. Eq. **16** describes a sigmoidal function that is steeper the higher the s (Fig. 1*B*). Therefore, for very reliable behaviors (high s, meaning individuals that are much more likely to make correct choices than erroneous ones), P_y grows fast with Δn and the deciding individual then goes to y with high probability when taking into account the behaviors of only very few individuals.

The behavior of the group is obtained by applying the decision rule in Eq. **16** sequentially to each individual (see *Methods*). After each behavioural choice, we update the number of individuals at x and y, using the new n_x and n_y for the next deciding individual (Fig. 1*C*, bottom). Repeating this procedure for all the individuals in the group, we can compute the probability for each possible final outcome of the experiment (Fig. 1*C*, top).

The relevance of the symmetric case is that the model has a single parameter and a single variable, enabling a powerful comparison against experimental data. We tested the model using an existing rich data set of collective decisions in three-spined sticklebacks [41], a shoaling fish species. This data set was obtained using a group of N_{tot} fish choosing between two identical refugia, one on their left and another on their right (Fig. 2*A*), equivalent to locations x and y in the model (Fig. 1*A*). At the start of the experiment, m_x (m_y) replica fish made of resin were moved along lines on the left (right) towards the refugia (Fig. 2*A*). The experimental results consisted on the statistics of collective decisions between the two refugia for 19 different cases using different group sizes $N_{\text{tot}} = 2$, 4 or 8 and different numbers of replicas going left and right, $m_x : m_y = \{1{:}1, 2{:}2, 0{:}1, 1{:}2, 0{:}2, 1{:}3, 0{:}3\}$ (Fig. 2*B*, blue histograms). To compare against these experimental data, we calculated the probability of finding a collective pattern applying the individual behavioural rule in Eq. **16** iteratively over each fish for the 19 experimental settings. We found a good fit of the model to the experimental data using for the 19 graphs the same value $s = 2.2$ (Fig. 2*B*, red line). The model is robust, with good fits in the interval $s = 2$-4 (Fig. S1). Despite the simplicity of the behavioral rule in Eq. **16**, it reproduces the experimental results, including the dependence on the total number of fish N_{tot}, even though the rule is independent of this parameter. The dependence on N_{tot} emerges from the application of the rule to the N_{tot} individuals in the group (Fig. S2). Note for example that the final experimental configuration located at the center of each graph (corresponding to half of the fish going to each side) is less likely the larger the group. Reaching the central state means that half of the fish selected the side that had fewer individuals at the moment they made the decision (taking the option with lower probability). As the group size increases, more fish must make the lower-probability choice to reach the central state, so its probability decreases even though there is no explicit influence of N_{tot} in Eq. **16** (compare Fig. S2*A* with Fig. 1*C*). Group decision-making in three-spined sticklebacks shows a single type of distribution of U-shape (or J-shape when there is a bias). However, the model in Eq. **16** also gives two other types of distributions, one bell-shaped and another M-shaped depending on the value of s and the number of animals in the group (Fig. S3).

Symmetric set-up with modified replicas of animals

An interesting modification of the experimental set-up consists in using replicas of the animals that we can modify to potentially alter their estimated reliability by the animals. We considered the particular case, mo-

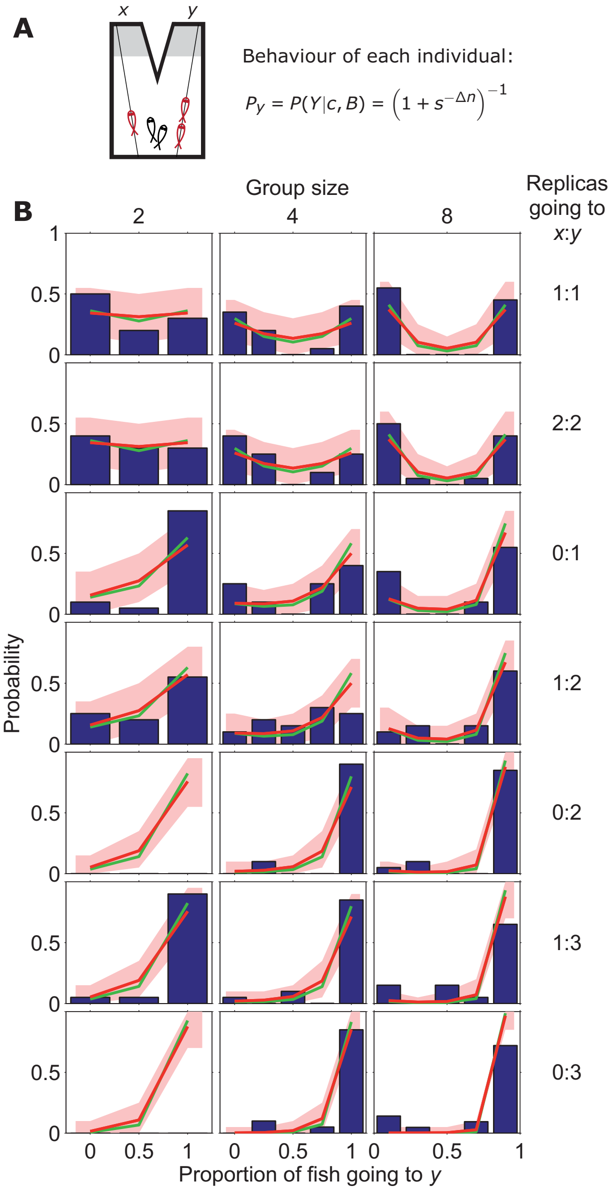

Figure 2. Comparison between the model and stickleback choices in symmetric set-up. (*A*) Schematic diagram of symmetric set-up with a group of sticklebacks (in black) choosing between two identical refugia and with different numbers of replica fish (in red) going to x and y. (*B*) Experimentally measured statistics of final configurations of fish choices from 20 experimental repetitions [41] (blue histogram) and results from the model in Eq. **16** in the main text (red line using reliability parameter $s = 2.2$; red region: 95% confidence interval; green line with $s = 2.6$). Different graphs correspond to different stickleback group sizes and different number of replicas going to x and y.

tivated by experiments in [42], of two types of modified replicas with different characteristics (for example, fat or thin), Fig. 3*A*. We considered 7 behaviors: 'animal goes to x' ($\beta_{\mathrm{f}x}$), 'animal goes to y' ($\beta_{\mathrm{f}y}$), 'most attractive replica goes to x' ($\beta_{\mathrm{R}x}$), 'most attractive replica goes to y' ($\beta_{\mathrm{R}y}$) 'least attractive replica goes to x' ($\beta_{\mathrm{r}x}$), 'least attractive replica goes to y' ($\beta_{\mathrm{r}y}$), and 'animal remains undecided' (β_{fu}). The probability of going to y in Eq. **11** then reduces to

$$P_y = \left(1 + a\, s_{\mathrm{f}x}^{n_{\mathrm{f}x}} s_{\mathrm{f}y}^{n_{\mathrm{f}y}} s_{\mathrm{R}x}^{n_{\mathrm{R}x}} s_{\mathrm{R}y}^{n_{\mathrm{R}y}} s_{\mathrm{r}x}^{n_{\mathrm{r}x}} s_{\mathrm{r}y}^{n_{\mathrm{r}y}} s_{\mathrm{fu}}^{N_{\mathrm{f}} - n_{\mathrm{f}x} - n_{\mathrm{f}y}}\right)^{-1}, \tag{17}$$

where subindex 'f' refers to real fish and 'R' ('r') to replicas of the most (least) attractive type. As in the previous section, symmetry imposes that $a = 1$ and $s_{\mathrm{fu}} = 1$. It also imposes the following relations between the reliability parameters, $s_{\mathrm{f}} \equiv s_{\mathrm{f}x} = 1/s_{\mathrm{f}y}$, $s_{\mathrm{R}} \equiv s_{\mathrm{R}x} = 1/s_{\mathrm{R}y}$, $s_{\mathrm{r}} \equiv s_{\mathrm{r}x} = 1/s_{\mathrm{r}y}$. Therefore,

$$P_y = \left(1 + s_{\mathrm{f}}^{-\Delta n_{\mathrm{f}}} s_{\mathrm{R}}^{-\Delta n_{\mathrm{R}}} s_{\mathrm{r}}^{-\Delta n_{\mathrm{r}}}\right)^{-1}, \tag{18}$$

where $\Delta n_{\mathrm{f}} \equiv n_{\mathrm{f}y} - n_{\mathrm{f}x}$, $\Delta n_{\mathrm{R}} \equiv n_{\mathrm{R}y} - n_{\mathrm{R}x}$ and $\Delta n_{\mathrm{r}} \equiv n_{\mathrm{r}y} - n_{\mathrm{r}x}$. In the particular case of only two different replicas, one going to x and the other to y and for notational simplicity taking the convention that the most (least) attractive replica goes to y (x), we have $\Delta n_{\mathrm{R}} = 1$ and $\Delta n_{\mathrm{r}} = -1$. Therefore,

$$P_y = \left(1 + \frac{s_{\mathrm{r}}}{s_{\mathrm{R}}} s_{\mathrm{f}}^{-\Delta n_{\mathrm{f}}}\right)^{-1}. \tag{19}$$

Note that the probability in Eq. **19** does not depend on s_{r} and s_{R} separately, but only on their ratio. Therefore, in this case the model uses only two parameters (s_{f} and $s_{\mathrm{r}}/s_{\mathrm{R}}$). We compared the model with the stickleback data set from [42], Fig. 3. The data in Fig. 3*B* has a different type of replica pair in each row, so in principle we would fit a different ratio $s_{\mathrm{r}}/s_{\mathrm{R}}$ for each row. But note that the first three rows correspond to experiments with the same three replicas (large, medium and small), combined in different pairs. The same can be said for the second and third threesomes of rows. Therefore, there are only two free parameters for each three rows. On the other hand, s_{f} should have the same value for all cases. The model again reproduces the experimental results reported in reference [42] , obtaining the best fit for $s_{\mathrm{f}} = 2.9$ (Fig. 3*B*). The result is robust, with good fits for $s_{\mathrm{f}} =$ 2-4 (Fig. S1) in accord with the value obtained for the case shown in Fig. 2*B*.

Asymmetric set-up

We finally considered the case in which sites x and y are different and the three behaviors are 'go to x' (β_x),

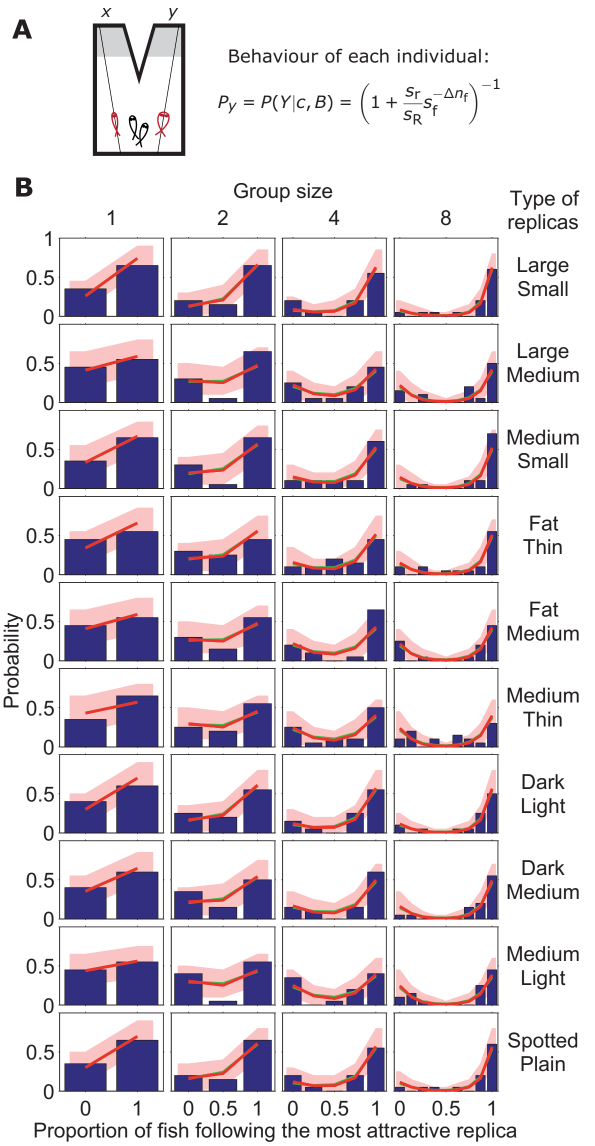

Figure 3. Comparison between the model and stickleback choices with two differently modified replicas. (*A*) Schematic diagram of symmetric set-up with a group of sticklebacks (in black) choosing between two identical refugia and with one replica fish going to x and a different one (in size, shape or pattern) going to y (in red). (*B*) Experimentally measured statistics of final configurations of fish choices from 20 experimental repetitions [42] (blue histogram) and results from cognitive model in Eq. **19** in the main text (red line using reliability parameter $s_{\mathrm{f}} = 2.9$ and $s_{\mathrm{r}}/s_{\mathrm{R}} = 0.35$, 0.7, 0.5, 0.52, 0.69, 0.75, 0.43, 0.55, 0.78, 0.43, for each row from top to bottom; red region: 95% confidence interval; green line with $s_{\mathrm{f}} = 2.6$ and same ratios $s_{\mathrm{r}}/s_{\mathrm{R}}$ as for red line). Different graphs correspond to different stickleback group sizes and different types of replicas going to x and y.

'go to y' (β_y) and 'remain undecided' (β_u). Eq. **11** reduces to

$$P_y = \left(1 + a\, s_x^{n_x} s_y^{n_y} s_u^{N-n_x-n_y}\right)^{-1}. \qquad (20)$$

The term $a = P(X|c)/P(Y|c)$ represents the non-social information and in general $a \neq 1$ because the set-up is asymmetric by design. This asymmetry might also affect how a deciding animal takes into account the behaviours of other animals depending on which side they chose, making in general $s_x \neq 1/s_y$. Also, undecision might be informative. For example, if non-social information indicates the possible presence of a predator at y, the undecision of other animals might confirm this to the deciding individual, further biasing the decision towards x. Therefore, we may have $s_u \neq 1$.

But it may also be the case that the set-up's asymmetry does not affect the social terms, so we also tested a simpler model in which $s \equiv s_x = 1/s_y$ and $s_u = 1$, giving

$$P_y = \left(1 + a\, s^{-\Delta n}\right)^{-1}. \qquad (21)$$

The stickleback dataset reported in reference [41] is ideally suited to test the asymmetric model for the experiments that were performed with a replica predator at the right arm (Fig. 4*A*). The model in Eq. **21** fits best the data with $s = 2.6$ (Fig. 4*B*) and it is robust with a good fit in $s = 2$-4 (Fig. S1). The more complex model in Eq. **20** gives fits very similar to those of simpler model. Specifically, parameter s_u was rejected by the Bayes Information Criterion [48], indicating that fish do not rely on undecided individuals. The fact that fish rely differently on other fish depending on the option they have taken could not be ruled out by the Bayes Information Criterion, but in any case the impact of this difference on the data is very small.

In the experiments in Fig. 2 and Fig. 4, we have assumed that the replicas are perceived by fish as real animals. However, it is reasonable to think that fish might perceive the difference, and rely differently on replicas and real fish. To test this, we considered different behaviors for fish and replicas, such as 'fish goes to x' and 'replica goes to x'. Making that distinction, we get that Eq. **11** reduces to

$$P_y = \left(1 + a\, s_{\mathrm{f}x}^{n_{\mathrm{f}x}} s_{\mathrm{f}y}^{n_{\mathrm{f}y}} s_{\mathrm{r}x}^{n_{\mathrm{r}x}} s_{\mathrm{r}y}^{n_{\mathrm{r}y}} s_{\mathrm{fu}}^{N_{\mathrm{f}}-n_{\mathrm{f}x}-n_{\mathrm{f}y}}\right)^{-1}. \qquad (22)$$

The Bayes Information Criterion rejects only parameter s_{fu}. However, the addition of the new parameters that distinguish replica from real fish give very small improvements in the fits compared to results of the simpler models in Eq. **16** and Eq. **21** (see Fig. S4 and Fig. S6), suggesting that fish follow replicas as much as they follow real fish.

Discussion

We have shown that probabilistic estimation in the presence of uncertainty can explain collective animal

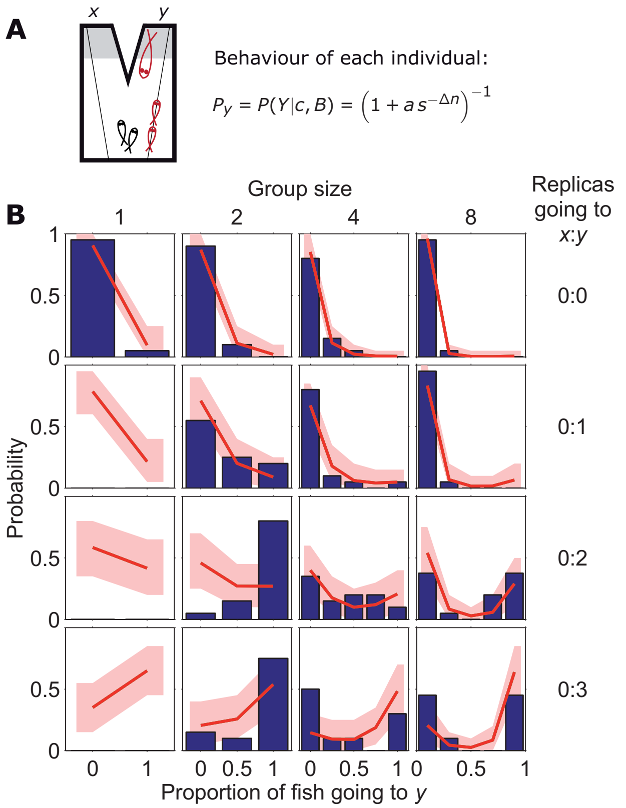

Figure 4. Comparison between the model and stickleback choices in asymmetric set-up. *A*) Schematic diagram of asymmetric set-up (predator at y, big fish depicted in red) with a group of sticklebacks (in black) choosing between two refugia, and replica fish (small fish depicted in red) going to y. (*B*) Experimentally measured statistics of final configurations of fish choices from 20 experimental repetitions [41] (blue histogram) and results from cognitive model in Eq. **21** in the main text (red line; $s = 2.6$, $a = 9.5$; red region: 95% confidence interval). Different graphs correspond to different stickleback group sizes and different number of replicas going to y.

decisions. This approach generated a new expression for each experimental manipulation, Eq. **16-21**, and was naturally extended to test for more refined cognitive capacities, Eq. **22**. The model was found to have a good correspondence with the data in three experimental settings (Figs. 2-4), always giving a good fit with the social reliability parameter s in the interval 2-4. Indeed, all the data have a very good fit with $s = 2.6$ (Figs. 2-3, green lines; red line in Fig. 4 is already for $s_x = 2.6$). For the the data used in this paper, previous empirical fits used more parameters [41] (Fig. S4 and Fig. S6, blue line), and added more complex behavioral rules when the basic model failed [42] (Fig. S5, blue line). Our approach thus gains in simplicity. It also finds an expression for each set-up with expressions for complex set-ups obtained with add-ons to those of simpler set-ups, making the model scalable and easier to understand in terms of simpler experiments.

Collective animal behavior has been subject to a particularly careful quantitative analysis. Previous studies have given descriptions led by the powerful idea that complex collective behaviors can emerge from simple individual rules. In fact, some systems have been found empirically to obey rules that are mathematically similar or the same as some of the ones presented in this paper, further supporting the idea that probabilistic estimation might underlie collective decision rules in many species. For example, a function like the one in Eq. **16** has been used to describe the behavior of Pharaoh's ant [49], a function like Eq. **21** for mosquito fish [50], and a function like the one in the right-hand-side of Eq. **21** for meerkats [51]. But despite the importance of group decisions in animals, little is known about the origin of such simple individual rules. This paper argues that probabilistic estimation can be an underlying substrate for the rules explaining collective decisions, thus helping in their evolutionary explanation.

Our model is naturally compatible with other theories that use a Bayesian formalism to study different aspects of behavior and neurobiology, thus contributing to a unified approach of information processing in animals. For example, it may be combined with the formalism of Bayesian foraging theory [18], through an expansion of the non-social reliability a. Related to this case, a very well studied example of use of social information is the one in which one individual can observe directly the food collected by another individual [28–32]. In this case, the social information is as unambigous as the non-social one, so in the end both types of information will have a similar mathematical form, in agreement with previous work [28–32]. Other kinds of social information (such as another individual's decision to leave a food patch or choices of females in mating [40]) would enter naturally in our reliability terms s_k. In discussing these and similar problems, it has been proposed that animals should use social information when their personal information is poor, and ignore it otherwise [25, 26, 40]. Our model provides a quantitative framework for this problem, predicting that social information is always used, only with different weights with respect to other sources of information. Bayesian estimation is also a prominent approach to study decisions in Neurobiology and Psychology [3–17] and it would be of interest to explore the mechanisms and role played by the multiplicative relation between non-social and social terms.

Our approach also makes a number of predictions. For example, it derives the probability of choosing among M options (see Eq. **S16** of the *Supporting*

Text), that for the symmetric case reduces to

$$P_\mu = \left(1 + \sum_{m \neq \mu}^{M} s^{-(n_\mu - n_m)}\right)^{-1}, \qquad (23)$$

predicted also to fit the data for cases with $M > 2$ options.

We also predict a quantitative link between estimation and collective behavior. The parameters a and s_k in our model are in fact not merely fitting parameters, but true experimental variables. Manipulations of a and s_k should allow to test that changes in collective behavior follow the predictions of the model. A counterintuitive prediction about the manipulation of s_k is that external factors unrelated to the social component can nevertheless modify it. For example, a fish that usually finds food in a given environment should interpret a sudden turn of one of his mates as an indication that it has found food, and therefore will follow it. In contrast, another fish that is not expected to find food in that environment will not interpret the sudden turn as indicative of food, and will not follow. Thus, the model predicts that the *a priori* probability of finding food (to which each fish can be trained in isolation) will modify its propensity to follow conspecifics. An alternative approach that would not need manipulation of the reliabilities s_k would consist in showing that the probability of copying a behavior increases with how reliably the behavior informs about the environment.

We can also extend the estimation model to use, instead of the location of animals, their predicted location. We would then find expressions like the ones in this paper but for the number or density of individuals estimated for a later time. Consider for example the case without non-social information, described in Eq. **16** for two options and in Eq. **23** for more options. We can rewrite these equations as $P_\mu = \Omega s^{n_\mu}$ with μ one of the options and Ω is the normalization, $\Omega = \sum_{m=1}^{M} s^{n_m}$, where M is the number of options. Then, we would have $P(\vec{x}) = \Omega s^{\rho(\vec{x};t+\Delta t)}$ for the continuous case using prediction. Future positions at times $t + \Delta t$ (where Δt does not need to be constant) in terms of variables at present time t would be given by $\vec{x} + \vec{v}\Delta t$ for animals moving at constant velocity $\vec{v}$. Consider then a simple case of an animal located at $\vec{x}$ and estimating the future position of a compact group at $\vec{x}_g$ and moving with velocity $\vec{v}_g$. The deciding animal would be predicted to move with a high probability in the direction $(\vec{x}_g(t) - \vec{x}(t)) + \Delta t \vec{v}_g(t)$. Estimation of future locations thus naturally predicts in this simple case a particular form of ‘attraction’ and ‘alignment’ forces of dynamical empirical models [45, 52] as attraction to future positions, but in the general also deviations from these simple rules.

Methods

Obtaining group behavior from the model of an individual

The estimation rules presented above refer to a single individual. To simulate the behavior of a group, we use the following algorithm: The current individual decides between x and y. After the decision, we recompute n_x and n_y and use the new values for the next deciding individual. The undecided individuals are only those that are waiting for their turn to decide. We tested an alternative implementation in which individuals may remain undecided or in which two individuals can decide simultaneously, obtaining no relevant differences. The file ’groupsimulator.m’, provided as *Supporting Data*, contains a Matlab function that runs the algorithm described above. This function has been used to generate all the theoretical results presented in this paper.

Fits

We computed log likelihood as the logarithm of the probability that the histograms come from the model. We searched for the model parameters giving a higher value of log likelihood, corresponding to a better fit.

Rejection of parameters

Parameters are rejected using the Bayesian information criterion [48] for model selection, which takes into account not only the goodness of fit of each model, but also the number of parameters. According to this criterion, among several models that have been fitted to maximize log likelihood, one should select the one in which

$$BIC = L - \frac{1}{2} k \log(h) \qquad (24)$$

is largest, where L is the log likelihood for the model, k is the number of parameters and h is the number of measurements.

Acknowledgments

We acknowledge useful comments by Sara Arganda, Larissa Conradt, Iain Couzin, Jacques Gautrais, David Sumpter, Guy Theraulaz, Julián Vicente Page and COLMOT 2010 participants. This work was funded by MICIIN (Spain) as Plan Nacional and as partners of the ERASysBio+ initiative supported under the EU ERA-NET Plus scheme in FP7, and by Biociencia program (CAM, Spain). A.P-E. acknowledges a FPU fellowship from MICINN (Spain).

A.P-E. and G.G.P. designed and performed the research, analyzed the data and wrote the paper.

References

1. Box G, Tiao G (1973) Bayesian inference in statistical analysis. New York: Addison-Wesley.
2. Jaynes ET, Bretthorst LG (2003) Probability Theory: The Logic of Science (Vol 1). Cambridge University Press.
3. Helmholtz H (1925) Physiological Optics, Vol. III: The perceptions of Vision. Rochester, NY, USA: Optical Society of America.
4. Mach E (1980) Contributions to the Analysis of the Sensations. Chicago, IL, USA: Open Court Publishing Co.
5. Knill DC, Pouget A (2004) The Bayesian brain: the role of uncertainty in neural coding and computation. Trends in neurosciences 27: 712–9.
6. Jacobs R (1999) Optimal integration of texture and motion cues to depth. Vision Research 39: 3621–3629.
7. Knill DC, Saunders JA (2003) Do humans optimally integrate stereo and texture information for judgments of surface slant? Vision Research 43: 2539–2558.
8. Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415: 429–33.
9. Battaglia PW, Jacobs RA, Aslin RN (2003) Bayesian integration of visual and auditory signals for spatial localization. Journal of the Optical Society of America A 20: 1391.
10. Alais D, Burr D (2004) The ventriloquist effect results from near-optimal bimodal integration. Current Biology 14: 257–262.
11. Gold JI, Shadlen MN (2001) Neural computations that underlie decisions about sensory stimuli. Trends in cognitive sciences 5: 10–16.
12. Kording KP, Wolpert DM (2004) Bayesian integration in sensorimotor learning. Nature 427: 244–247.
13. Körding KP, Wolpert DM (2006) Bayesian decision theory in sensorimotor control. Trends in cognitive sciences 10: 319–26.
14. Gold JI, Shadlen MN (2007) The neural basis of decision making. Annual review of neuroscience 30: 535–74.
15. Courville AC, Daw ND, Touretzky DS (2006) Bayesian theories of conditioning in a changing world. Trends in cognitive sciences 10: 294–300.
16. Kruschke JK (2006) Locally Bayesian learning with applications to retrospective revaluation and highlighting. Psychological review 113: 677–99.
17. Tenenbaum JB, Kemp C, Griffiths TL, Goodman ND (2011) How to Grow a Mind: Statistics, Structure, and Abstraction. Science 331: 1279–1285.
18. Oaten A (1977) Optimal foraging in patches: A case for stochasticity. Theoretical Population Biology 12: 263–285.
19. Biernaskie JM, Walker SC, Gegear RJ (2009) Bumblebees learn to forage like Bayesians. The American naturalist 174: 413–423.
20. Alonso J (1995) Patch use in cranes: a field test of optimal foraging predictions. Animal Behaviour 49: 1367–1379.
21. McNamara JM, Green RF, Olsson O (2006) Bayes theorem and its applications in animal behaviour. Oikos 112: 243–251.
22. Valone TJ (2006) Are animals capable of Bayesian updating? An empirical review. Oikos 112: 252–259.
23. Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. Philosophical transactions of the Royal Society of London Series B, Biological sciences 357: 1549–57.
24. Blanchet S, Clobert J, Danchin E (2010) The role of public information in ecology and conservation: an emphasis on inadvertent social information. Annals of the New York Academy of Sciences 1195: 149–68.
25. Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends in ecology & evolution 20: 187–93.
26. Giraldeau LA, Valone TJ, Templeton JJ (2002) Potential disadvantages of using socially acquired information. Philosophical transactions of the Royal Society of London Series B, Biological sciences 357: 1559–66.

27. Wagner RH, Danchin E (2010) A taxonomy of biological information. Oikos 119: 203–209.

28. Valone TJ (1989) Group Foraging, Public Information, and Patch Estimation. Oikos 56: 357–363.

29. Templeton JJ, Giraldeau LA (1995) Patch assessment in foraging flocks of European starlings: Evidence for the use of public information. Behavioral Ecology 6: 65–72.

30. Templeton JJ, Giraldeau LA (1996) Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. Behavioral Ecology and Sociobiology 38: 105–14.

31. Smith JW, Benkman CW, Coffey K (1999) The use and misuse of public information by foraging red crossbills. Behavioral Ecology 10: 54–62.

32. Clark C, Mangel M (1986) The evolutionary advantages of group foraging. Theoretical Population Biology 30: 45–75.

33. Doligez B, Danchin E, Clobert J (2002) Public information and breeding habitat selection in a wild bird population. Science (New York, NY) 297: 1168–70.

34. Boulinier T, Danchin E (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evolutionary Ecology 11: 505–517.

35. Coolen I, van Bergen Y, Day RL, Laland KN (2003) Species difference in adaptive use of public information in sticklebacks. Proceedings Biological sciences / The Royal Society 270: 2413–9.

36. van Bergen Y, Coolen I, Laland KN (2004) Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. Proceedings Biological sciences / The Royal Society 271: 957–62.

37. Rieucau G, Giraldeau La (2009) Persuasive companions can be wrong: the use of misleading social information in nutmeg mannikins. Behavioral Ecology 20: 1217–1222.

38. Lima SL (1995) Collective detection of predatory attack by social foragers: fraught with ambiguity? Animal Behaviour 50: 1097–1108.

39. Proctor CJ, Broom M, Ruxton GD (2001) Modelling antipredator vigilance and flight response in group foragers when warning signals are ambiguous. Journal of theoretical biology 211: 409–17.

40. Nordell, Valone TJ (1998) Mate choice copying as public information. Ecology Letters 1: 74–76.

41. Ward AJW, Sumpter DJT, Couzin ID, Hart PJB, Krause J (2008) Quorum decision-making facilitates information transfer in fish shoals. Proceedings of the National Academy of Sciences of the United States of America 105: 6948–53.

42. Sumpter DJT, Krause J, James R, Couzin ID, Ward AJW (2008) Consensus decision making by fish. Current Biology 18: 1773–1777.

43. Couzin ID, Krause J (2003) Self-organization and collective behavior in vertebrates. Advances in the Study of Behavior 32: 1–75.

44. Sumpter DJT (2006) The principles of collective animal behaviour. Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences 361: 5–22.

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

46. Gaissmaier W, Schooler LJ (2008) The smart potential behind probability matching. Cognition 109: 416–22.

47. Wozny DR, Beierholm UR, Shams L (2010) Probability matching as a computational strategy used in perception. PLoS Computational Biology 6: 7.

48. Schwarz G (1978) Estimating the dimension of a model. Annals of Statistics 6: 461–464.

49. Jeanson R, Ratnieks FLW, Deneubourg JL (2003) Pheromone trail decay rates on different substrates in the Pharaoh's ant, Monomorium pharaonis. Physiological Entomology 28: 192–198.

50. Ward AJW, Herbert-Read JE, Sumpter DJT, Krause J (2011) Fast and accurate decisions through collective vigilance in fish shoals. PNAS 108: 6–9.

51. Bousquet CAH, Sumpter DJT, Manser MB (2010) Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups. Proceedings of the Royal Society B Biological Sciences in press.

52. Couzin ID, Krause J, James R, Ruxton GD, Franks NR (2010) Collective memory and spatial sorting in animal groups. Journal of Theoretical Biology 218: 1–11.

Supporting Figures

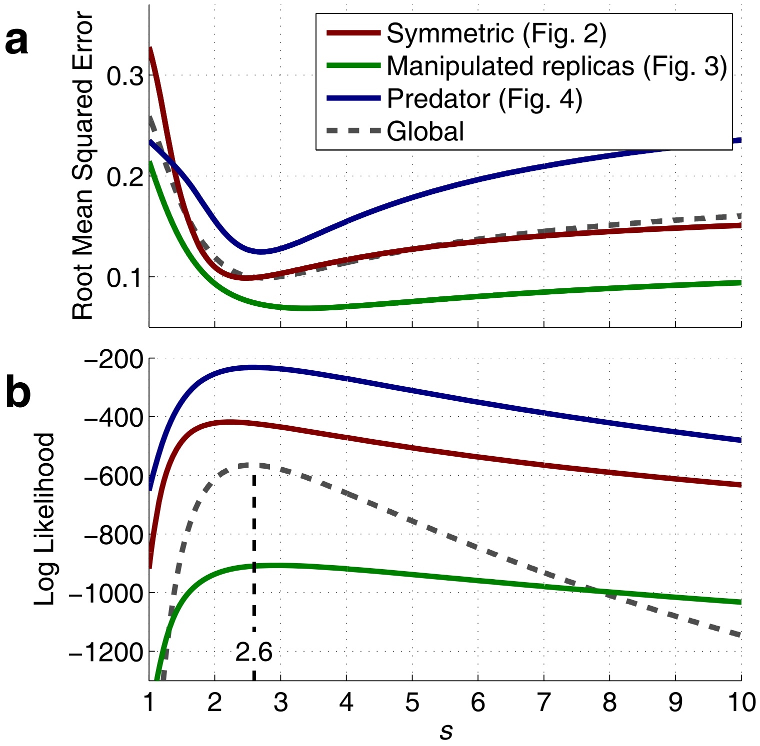

Figure S1. Goodness of fit for different values of the reliability (s). Red: Symmetric case (plots in Fig. 2 in the main text). **Green:** Case with different replicas at each side (plots in Fig. 3 in the main text. The ratios $s_{\mathrm{r}}/s_{\mathrm{R}}$ for each case are fixed in the values specified in the figure caption of Fig. 3 or Fig. S4). **Blue:** Asymmetric set-up with predator on one side (plots in Fig. 4 in the main text. $a = 9.5$) **a.** Root mean squared error between the data and the probabilities predicted by the model. Grey dashed line shows the mean RMSE for the three cases. The absolute values for each case depend on the shape of the data and are not comparable, only the trends and the position of the minima should be compared. **b.** Logarithm of the probability that the data come from the model. The height of each curve depends on the number of data for each experiment, only the trend and the position of the maxima should be compared. Grey dashed line shows the sum of the three coloured lines, but shifted by 1000 so that it fits on the scale. The peak of this global probability indicates the value of s that best fits the three datasets ($s = 2.6$).

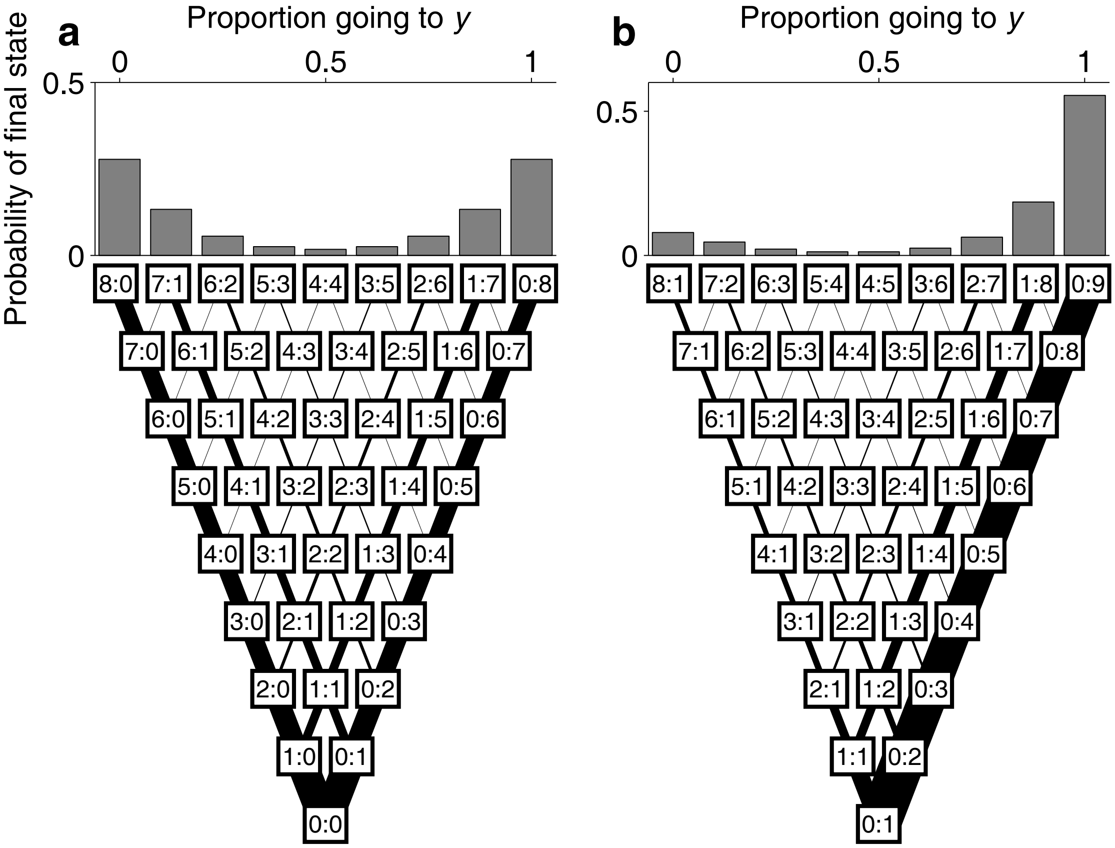

Figure S2. Illustration of the decision-making process. Bottom: Decision-making process, according to Eq. **16** in the main text (with $s = 2.5$). Time runs from bottom to top. Each box represents a state with a given number of fish having already decided x or y ($n_x : n_y$). Each state can lead to another two states in the following time step, depending on whether the focal fish decides to go to x or y. The width of the lines connecting states is proportional to the probability of that transition (equal to the probability of the prior state times the probability of the focal fish making the decision that leads to the later one). **Top:** Probability of each state after 8 fish have made their decisions. **a.** Case with no replicas, in which the final outcome is U-shaped. Note that the central states' probability decreases as more fish make their decision, not because of an explicit effect of the total number of fish in the probabilities, but because they accumulate more and more unlikely choices. **b.** Case with one replica going to y (so initial state is already 0:1), in which the final outcome is J-shaped.

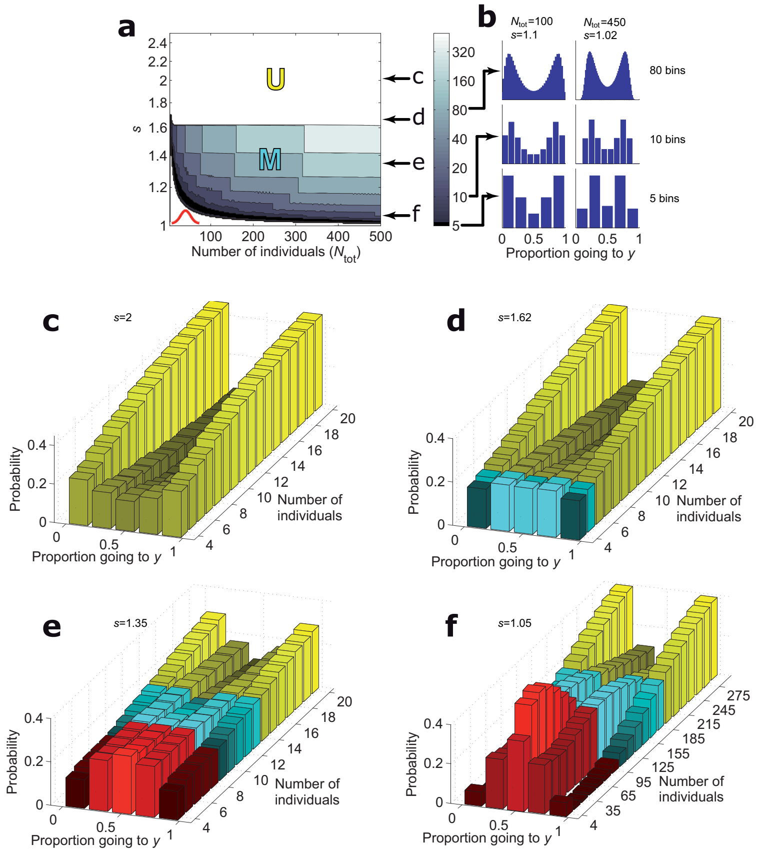

Figure S3. Prediction of the dynamics for different values of the reliability parameter s and the group size. The histogram for the probability of final states may have three main shapes: Bell shape, in which central states have maximum probability, decreasing monotonously towards the edges. U shape, in which the central states have minimum probability, and increases monotonously towards the edges. And an intermediate M shape, in which the maximum probability is at points located between the center and the edges of the histogram. **a.** Shape of histogram as a function of s and the group size. For non-social behavior ($s = 1$) the histogram is bell-shaped, due to combinatorial effects. However, a bell-shape is also compatible with social animals, for a certain range of s and group size (white region on the bottom-left). For higher values of s and group size the histograms are M-shaped (region coloured in black and blue). However, the observation of the M shape depends on the number of bins, because the drop in probability near the edge or in the center may be masked if the binning is too coarse, producing a bell-shaped or U-shaped histogram. This is an important practical issue, because the amount of data that can be collected rarely allows more than 5 bins. The colorscale reflects the number of bins needed to observe the M shape (black has been reserved for exactly 5 bins). For high values of s the histograms have U shape (white region on the top). Also, all the M-region above the black zone becomes U when the binning is too coarse. There is also a tiny region below the black zone where the M shape becomes a bell when the binning is too coarse. **b.** Dependence of the apparent shape on the number of bins: Top, 80 bins. Middle, 10 bins. Bottom, 5 bins. On the left, a probability that seems U-shaped for 5 bins, but is M shaped for a higher number of bins. On the right, a probability that stays M-shaped for any number of bins. **c-f.** Dynamics of the probability as the individuals of the group make their decisions. As Eq. **16** in main text does not depend on group size, this evolution can be understood as moving horizontally in the map of box (a). For high s, the probability has U shape from the beginning, becoming more pronounced as more individuals decide (box c, $s = 2$). There is a small interval of s where the probability has a small and shallow M-shaped transient and then becomes U-shaped (box d, $s = 1.62$). For low s, there is a first stage with bell-shaped probability, then a second stage with M-shaped probability and finally the U-shaped probability, that also becomes more pronounced as more individuals decide. The first two stages are more pronounced (and therefore more easily observable) the lower the s (compare $s = 1.35$ in box e with $s = 1.05$ in box f).

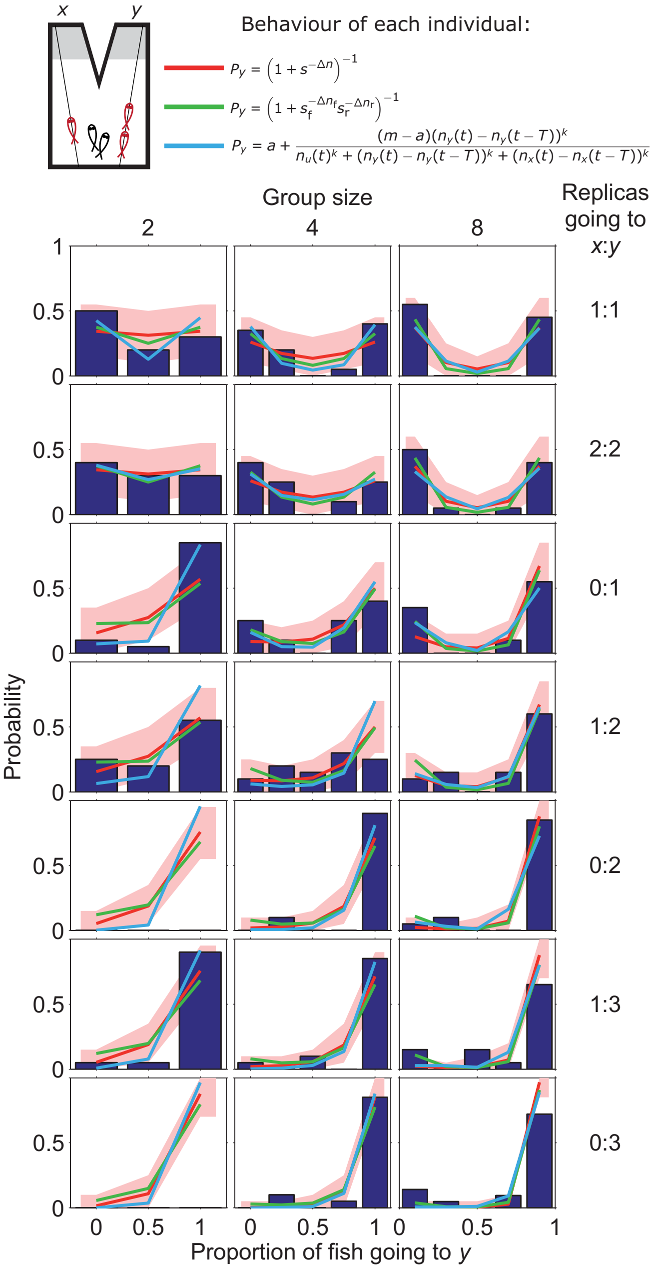

Figure S4. Comparison between different models for the symmetric set-up. Experimentally measured statistics of final configurations of fish choices from 20 experimental repetitions [41] (blue histograms). Red line: results from cognitive model in Eq. **16** in the main text ($s = 2.2$; red region: 95% confidence interval). Green line: Enhanced model with different reliability for the replicas ($s_{\mathrm{f}} = 3$, $s_{\mathrm{r}} = 1.76$). Blue line: Empirical model presented in Ref. [41]. Different graphs correspond to different stickleback group sizes and different number of replicas going to x and y.

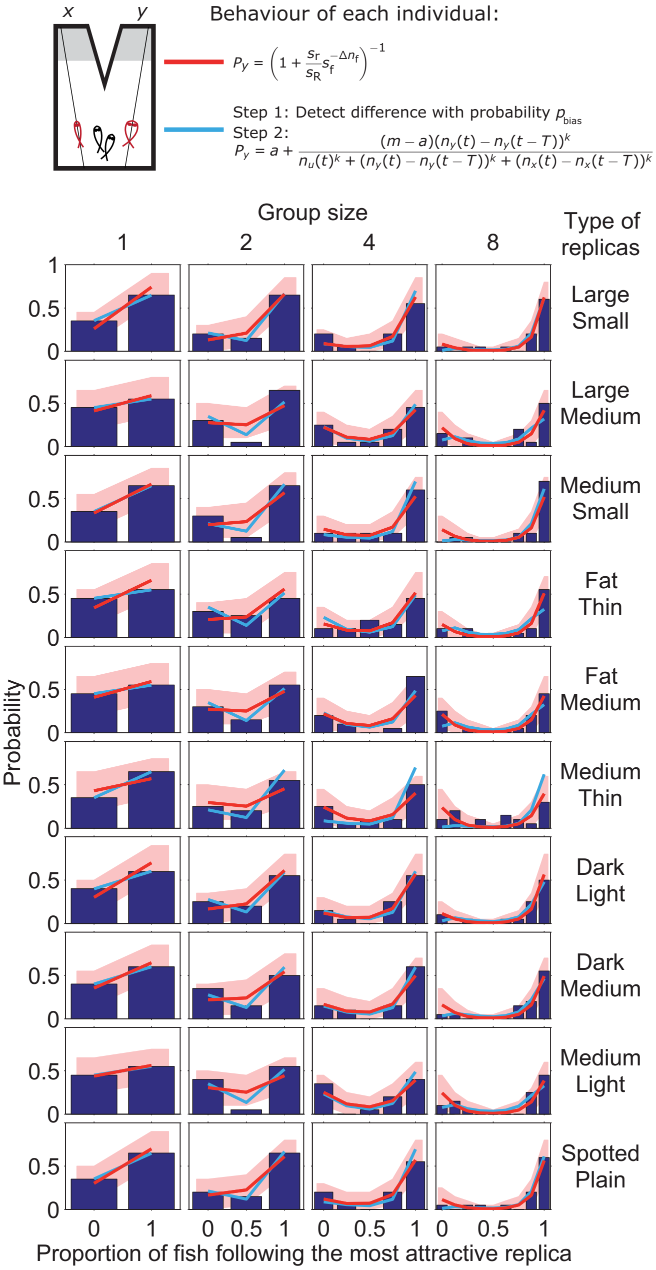

Figure S5. Comparison between different models for the condition with two different replicas. Experimentally measured statistics of final configurations of fish choices from 20 experimental repetitions [42] (blue histograms). Red line: results from estimation model in Eq. **19** in the main text ($s_{\mathrm{f}} = 2.9$, $s_{\mathrm{r}}/s_{\mathrm{R}} = 0.35, 0.7, 0.5, 0.52, 0.69, 0.75, 0.43, 0.55, 0.78, 0.43$ for each row from top to bottom; red region: 95% confidence interval). Blue line: Empirical model presented in Ref. [42]. Different graphs correspond to different stickleback group sizes and different types of replicas going to x and y.

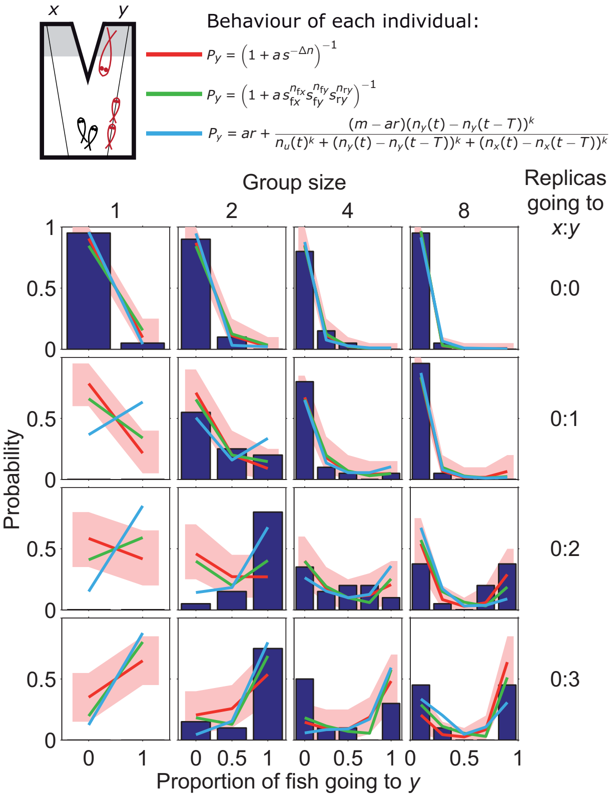

Figure S6. Comparison between different models in the asymmetrical set-up. Experimentally measured statistics of final configurations of fish choices from 20 experimental repetitions [41] (blue histograms). Red line: results from estimation model in Eq. **21** in the main text ($s = 2.6$, $a = 9.5$; red region: 95% confidence interval). Green line: Enhanced model with different reliability for the fish going to different locations and for the replicas ($a = 5.5$, $s_{\mathrm{f}x} = 50$, $s_{\mathrm{f}y} = 2/3$, $s_{\mathrm{r}y} = 0.36$. $s_{\mathrm{r}x}$ has no effect because there are no replicas going to x). Blue line: Empirical model presented in Ref. [41]. Different graphs correspond to different stickleback group sizes and different number of replicas going to y.

Supporting text: Model for more than 2 options

We present a derivation of the model for the more general case of M different options (instead of the 2 options used in the main text). We also discuss some particular cases that give simple expressions while still widely applicable.

General model for M options

Let M be the number of possible options, y_m, $m = 1 \dots M$. Each individual estimates the probability that each option is the best one, using its non-social information (c) and the behavior of the other individuals (B). So for one given option, say y_μ, we want to compute

$$P(Y_\mu|c, B), \tag{S1}$$

where Y_μ stands for 'y_μ is the best option'. We can compute the probability in Eq. **S1** using Bayes' theorem,

$$P(Y_\mu|c, B) = \frac{P(B|Y_\mu, c)P(Y_\mu|c)}{\sum_{m=1}^{M} P(B|Y_m, c)P(Y_m|c)}. \tag{S2}$$

Dividing numerator and denominator by the numerator, we get

$$P(Y_\mu|c, B) = \frac{1}{\sum_{m=1}^{M} a_{m\mu} S_{m\mu}}, \tag{S3}$$

where

$$a_{m\mu} = \frac{P(Y_m|c)}{P(Y_\mu|c)} \tag{S4}$$

contains only non-social information, and

$$S_{m\mu} = \frac{P(B|Y_m, c)}{P(B|Y_\mu, c)} \tag{S5}$$

contains the social information. Note that each term of the summation preserves the multiplicative relation between social and non-social information that was also apparent in Eq. 3 of the main text. There may be $M-1$ independent non-social parameters $a_{m\mu}$ in the case that no two options have equal non-social information. But usually this will not be the case, and the number of independent non-social parameters will be lower.

Now we assume independence among behaviors (Eq. 6 in main text), and group all possible behaviors in K classes, $\{\beta_k\}_{k=1}^{K}$ (Eq. 7 in main text). These two assumptions transform Eq. **S5** into

$$S_{m\mu} = \prod_{k=1}^{K} s_{k,m\mu}^{n_k}, \tag{S6}$$

where n_k is the number of individuals performing behavior β_k, and

$$s_{k,m\mu} = \frac{P(\beta_k|Y_m, c)}{P(\beta_k|Y_\mu, c)} \tag{S7}$$

are the reliability parameters for behavior β_k with respect to options y_m and y_μ. There may be up to $K(M-1)$ independent reliability parameters but usually they will not be all independent.

In summary, from Equations **S3** and **7** we have that

$$P(Y_\mu|c, B) = \left(\sum_{m=1}^{M} a_{m\mu} \prod_{k=1}^{K} s_{k,m\mu}^{n_k} \right)^{-1}. \tag{S8}$$

This equation summarizes the general model applicable to any kind of experiment. In the following sections we consider two particular cases with a much simpler expression.

One basic reliability parameter

The general model in Eq. **S8** depends in general on $K(M-1)$ independent reliability parameters $s_{k,m\mu}$. Here we derive the model for a particular case in which there is only one reliability parameter, s.

First, we consider classes of behaviors (from now on we call them just 'behaviors') that simply consist of choosing a given option. If for example the options are different places, behaviors would be going to each of those places. Therefore, the number of possible behaviors is the same as the number of options, $K = M$. We use the convention that β_j is 'choosing option y_j'. Note that when a behavior is not informative (i.e. its reliability parameter is 1) it has no impact on the model in Eq. **S8**. Therefore, considering this set of behaviors is equivalent to assuming that all other behaviors have reliability parameter equal to 1.

We further assume that $P(\beta_k|Y_m, c)$ only depends on whether $k = m$ or $k \neq m$, so that

$$\begin{aligned} P(\beta_k|Y_k, c) &= P(\beta_l|Y_l, c) \\ P(\beta_k|Y_m, c) &= P(\beta_l|Y_p, c), \quad k \neq m,\ l \neq p \end{aligned} \tag{S9}$$

Note that $P(\beta_k|Y_k, c)$ is the probability that another individual makes the correct choice, and $P(\beta_k|Y_m, c) with\ k \neq m$ is the probability that it makes a wrong choice. So this assumption means that the probability of making the correct choice is the same regardless of which option is actually the correct one. In the case of symmetric choices, in which non-social information c is the same for all options, this relation will hold automatically, not being an extra assumption. It is likely that it also holds for many asymmetric choices. For example, the results for the asymmetric set-up presented in the main text suggest that it holds in that case. We define

$$\begin{aligned} p_c &\equiv P(\beta_k|Y_k, c) \\ p_f &\equiv P(\beta_k|Y_m, c), \quad k \neq m. \end{aligned} \tag{S10}$$

As it only matters whether the behavior matches the correct choice or not, there are only four distinct types of reliability parameters $s_{k,m\mu}$ (Eq. **S7**):

$$\begin{aligned} s_{k,kk} &= \frac{P(\beta_k|Y_k, c)}{P(\beta_k|Y_k, c)} = \frac{p_c}{p_c} = 1 \\ s_{k,ml} &= \frac{P(\beta_k|Y_m, c)}{P(\beta_k|Y_l, c)} = \frac{p_f}{p_f} = 1, \quad k \neq m,\ k \neq l \\ s_{k,km} &= \frac{P(\beta_k|Y_k, c)}{P(\beta_k|Y_m, c)} = \frac{p_c}{p_f} = s, \quad k \neq m \\ s_{k,mk} &= \frac{P(\beta_k|Y_m, c)}{P(\beta_k|Y_k, c)} = \frac{p_f}{p_c} = \frac{1}{s}, \quad k \neq m, \end{aligned} \tag{S11}$$

where

$$s \equiv \frac{p_c}{p_f} \tag{S12}$$

is the basic reliability parameter, equal to the probability that another individual makes the correct choice over the probability that it makes a mistake, for any behavior and for any individual. We regroup the terms inEq. **S8** so that it reflects the different types of $s_{k,m\mu}$ (Eq. **S11**), and get

$$P(Y_\mu|c, B) = \left(\sum_{m=1}^{M} a_{m\mu} s_{m,m\mu}^{n_m} s_{\mu,m\mu}^{n_\mu} \prod_{\substack{k=1 \\ k\neq m \\ k \neq \mu}}^{K} s_{k,m\mu}^{n_k} \right)^{-1}. \tag{S13}$$

Using the relations in Eq. **S11** we have that

$$P(Y_\mu|c, B) = \left(\sum_{m=1}^{M} a_{m\mu} s^{-(n_\mu - n_m)} \right)^{-1}. \tag{S14}$$

Note that the term $m = \mu$ is always equal to 1, so Eq. **S14** is identical to

$$P(Y_\mu|c, B) = \left(1 + \sum_{\substack{m=1 \\ m\neq\mu}}^{M} a_{m\mu} s^{-(n_\mu - n_m)} \right)^{-1}, \tag{S15}$$

that has the same structure as the equations presented in the main text.

Symmetric case

In the special case that all options are indistinguishable using non-social information alone (symmetric case), all non-social parameters $a_{m\mu}$ are equal 1 and Eq. **S15** becomes

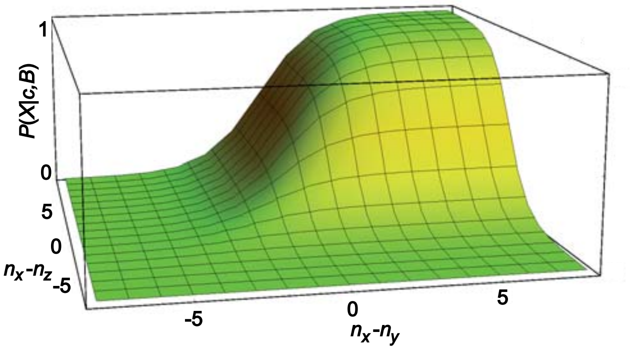

Figure S7. Probability of choosing one of the options for the 3-choice symmetric case.

$$P(Y_\mu|c, B) = \left(1 + \sum_{\substack{m=1 \\ m\neq\mu}}^{M} s^{-(n_\mu - n_m)} \right)^{-1}. \tag{S16}$$

We recall that in this case Eq. **S9** holds automatically, not being an extra assumption.

In the particular case of 3 options, x, y, z, we have

$$P(X|c, B) = \left(1 + s^{-(n_x - n_y)} + s^{-(n_x - n_z)} \right)^{-1}, \tag{S17}$$

and the corresponding expressions for $P(Y|c, B)$ and $P(Z|c, B)$. Fig. S7 shows $P(X|c, B)$ in terms of its two effective variables, $n_x - n_y$ and $n_x - n_z$ (Eq. **S17**).