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Effect of social information on an individual's assessment of its environment

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That observed behaviours conflate information processing with resulting responses presents a challenge for understanding how social information contributes to adaptive behaviour in animals. Here, we develop a mathematical model that isolates how individuals assess their environment and use it to examine how social information impacts those assessments. We consider the influences of personal and social sampling efforts, how individuals combine these sources of information, group size, social sampling practices and types of environmental variation. Our analyses lead to predictive formulas that show that social information often improves but sometimes impairs environmental assessments and that the magnitude of improvement or diminishment increases with the extent of environmental variation. We also show that the weight an individual gives to social information affects both whether it improves or degrades its assessment as well as the size of that effect. Simulation results show that group size does not affect the influence of social information on average but does affect the variability of those influences.
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Animals make behavioural decisions throughout their lives, including when and where to forage, mate, disperse and migrate. As the fitness consequences of these decisions frequently depend on environmental conditions that can vary over time and space, animals often gather information about the environment to inform behavioural decisions (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). Animals can collect such information by directly sampling from their environment (hereafter personal information), or indirectly by monitoring the behaviours of others (social information; Danchin, Giraldeau, Valone, & Wagner, 2004; Valone & Templeton, 2002). Indeed, evidence has now accumulated that animals can combine personal information with social information in a range of behavioural decisions including those related to foraging (Brown, 1988; Coolen, Ward, Hart, & Laland, 2005; Smith, 1999), selection of breeding sites (Doligez, 2002; Parejo, White, Clobert, Dreiss, & Danchin, 2007; Ward, 2005), mate choices (White, 2004), reproductive allocations (Fletcher & Miller, 2008) and aggressive interactions (Oliveira, McGregor, & Latruffe, 1998). And although social information can improve decision making (Valone & Templeton, 2002), this is not always the case (Feldman, Aoki, & Kumm, 1996; Giraldeau, Valone, & Templeton, 2002; Rieucau & Giraldeau, 2011).

The value that any information provides in behavioural decision making reflects both the extent to which the information reduces ambiguity about environmental conditions and the costs associated with collecting that information (Dall et al., 2005). Thus, the extent to which animals rely on the information they collect directly versus socially likely reflects both the extent to which each reduces ambiguity and the cost of acquiring the information. Indeed, social information has often been suggested to reduce ambiguity at low costs relative to information collected directly (Dawson & Chittka, 2014; Webster & Laland, 2008). In the present study, we are interested in evaluating the conditions under which social information does or does not reduce ambiguity about environmental conditions, irrespective of costs.

From a proximate perspective, the process by which animals arrive at information-based behavioural decisions can be viewed as multistep (Blumstein & Bouskila, 1996). First, information is gathered and used to make an assessment of the environment. Then, a decision rule is applied to this assessment to generate a behavioural response. Yet, studies in behavioural ecology have rarely examined the steps of information assessment and decision making separately (Blumstein & Bouskila, 1996; Valone, 2007). From a practical point of view, it is frequently difficult to devise empirical experiments that allow for the evaluation of information assessment independently of the application of a decision rule. However, if we

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wish to evaluate the value of social information with respect to reducing ambiguity about the environment, then we suggest that the assessment step is a key point for focus.

Here, we develop a mathematical model to study the often obscured process of assessment separately from decision making. Our goal is to better understand how social information impacts ambiguity about the environment. Models are an established scientific means to study components of a system that are present but not directly visible. Mathematical models in particular allow one to apply mathematical reasoning to discover logical consequences of assumptions; the result is both a rigorous understanding of the assumed processes as well as logically sound hypotheses that can be compared with empirical observations to test assumptions. We use our mathematical model of information assessment to ask the following: when does social information improve the accuracy of an individual's assessment and by how much? We address these questions by comparing the accuracy of an individual's assessment of the environment based solely on its own sampling to that of its assessment based on combining social information with its own. Our modelling framework allows us to explore various ways that individuals can collect and use social information to form assessments of environmental conditions. Specifically, we examine the impact of social information on ambiguity under varying (1) distributions of the environment, (2) intensities of direct and social information sampling and (3) means by which direct and social information are combined.

MODEL

Our model imagines a group of N animals, each seeking to assess an environmental state such as the abundance of a key resource or the risk of predation in the group's surroundings. We assume each individual gathers information about the state of the environment both directly from the environment and indirectly from others in the group and combines the two sources to make an integrated inference.

For simplicity, we assume that each individual directly samples its environment (i.e. collects personal information) independently. An individual's direct samples might consist of its visual or olfactory observations of the resource/risk or a set of behavioural probes. We refer to the assessment an individual would make based solely on this information as its ‘personal assessment’.

We also assume that each individual collects indirect information about the environment from one or more social partners. The modality by which this indirect social information is acquired may be completely different from that of its personal information. For example, an individual's personal information may be based on a visual inspection of its environment whereas its social information may come from attributes of its neighbours' vocalizations or ascertainments of their general activity levels.

Instead of specific forms of private and social information, our model focuses on consequences of a more basic assumption, namely, that an individual's information derives from two different sources: itself and others. This distinction is fundamental to understanding the biology of environmental assessment because these two sources may differ substantially in the nature of the information they provide and their availability. We use the term ‘combined assessment’ in reference to the assessment an individual makes about the environment by combining its social information with its personal information. Comparing this to the individual's personal assessment reveals the value its social information adds.

Our model envisions the assessment of an environmental state that is locally distributed with mean μ and variance σ^2 and that each individual aims to assess the mean state, μ. The state of the environment could be continuous or discrete. Examples of continuous environmental variation include temperature, salinity, moisture, nutrient content, predation risk or the concentration of a toxin. Examples of discrete environmental variation include presence versus absence (of a predator, food resource, habitat feature, etc.) or distinct sizes or states (large versus small, wet versus dry, toxic versus nontoxic, etc.). In the case of a dichotomous discrete environmental state, such as the presence or absence of a predator, the mean μ is identical to the probability of observing a given state, such as the presence of a predator. In this case, the variance is perhaps less intuitive than for a continuous environment, but it likewise quantifies uncertainty about the environmental state.

The model considers three separate quantities that describe how an individual collects and processes information from its environment: K, the size of its direct sample (i.e. personal information), K_S, the number of social samples it gathers (social information), and w, the relative weight an individual gives to its social information when forming its combined assessment (these and other parameters are summarized in Table 1).

Collecting and Processing Information

We explored the influence of social information by comparing assessments of the environment based on personal information alone to those combined with social information. To that end, our model contains three phases (Fig. 1a). First, individuals collect personal information and, second, collect social information. Third, they use both sources of information to form a combined assessment of the environmental state.

In the first phase of the model, each animal randomly samples the environment K times. These observations are used to form its personal assessment of the mean environmental state, μ, which we assume to be the mean of its personal sample. Although such an assessment could conceivably be made in almost any way, we use the sample mean here for biological and statistical reasons: empirical evidence suggest that animals combine information using the sample mean (De Corte & Matell, 2016; Devenport & Devenport, 1994; Wystrach, Mangan, & Webb, 2015) and, from statistics, it is known that the sample mean is the best linear unbiased estimator of the distribution mean μ (e.g. Casella & Berger, 2002). Future studies could use our overall approach to investigate alternative forms of assessment.

Let X_{ij} denote the jth sample of the environment obtained by individual i where $j = 1, 2, \ldots, K$ and $i = 1, 2, \ldots, N$ for a group of size N. The mean of individual i's personal samples – its personal assessment – is

$$e_{p_i} = \frac{1}{K}\sum_{j=1}^{K} X_{ij} . \quad (1)$$

Since social information may assume a vast array of forms (Bailey, 2011; Manassa, McCormick, Chivers, & Ferrari, 2013; O'Mara, Dechmann, & Page, 2014), we sought to represent it for the second phase of the model in a flexible way that is inclusive of an extensive diversity of biological scenarios. Specifically, the model

Table 1
Model parameters

Parameter	Definition
K	Number of times the environment is directly sampled
K_s	Number of social samples gathered
w	Social information weight
N	Group size
μ	Mean environmental state
σ^2	Variance of the environmental state

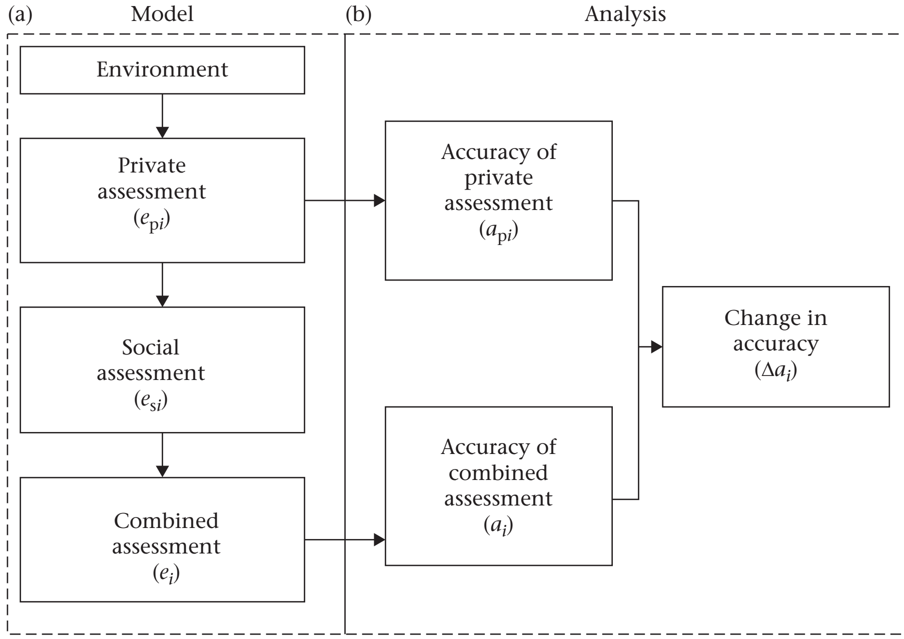

Figure 1. Model components and analyses. (a) Individuals collect personal and social information and then combine both sources of information to produce a combined assessment of the environment. (b) Analyses compare the accuracy of an individual's combined assessment to the accuracy of the assessment based solely on its personal information.

assumes all individuals present public cues (such as a vocalization, pheromone, morphological condition or behaviour) that reflect some or all of their personal samples of the environmental state. Let Y_{ij} denote the jth of K_S social samples presented to individual i and let its 'social assessment', e_{s_i}, be the mean of its social samples:

$$e_{s_i} = \frac{1}{K_S} \sum_{j=1}^{K_s} Y_{ij}. \tag{2}$$

This model is quite general in that it does not specify how the K_S social samples originate and so it applies to a large number of ways that social information might be collected. An individual's social samples may be obtained from K_S different social partners, from a smaller subset of partners, or even from a single partner. The social samples themselves may be collected as isolated observations of a partner's personal samples or via a composite indicator that integrates several of a partner's personal samples. For example, suppose an individual observes a cue from a social partner, such as its body condition, that reflects the partner's personal assessment of the environment, e_{p_i} (equation 1). Even though the focal individual observes none of its partner's K environmental samples directly, its social sample size would be $K_S = K$ in this case; the social samples of the focal individual would be the personal samples of the observed social partner. We consider potential impacts of different scenarios below for drawing K_S social samples, involving anywhere from one up to K_S distinct social partners.

Finally, each individual combines its personal and social assessments to form its combined assessment of the environment, denoted e_i for individual i. We assume each individual gives the social assessment (equation 2) weight w ($0 \leq w \leq 1$) and personal assessment (equation 1) weight $1 - w$ resulting in combined assessment

$$e_i = we_{s_i} + (1 - w)e_{p_i}. \tag{3}$$

The weight w could represent any number of internal or external factors that contribute to an individual's collective evaluation. For example, w might reflect the relative confidence an individual has in the information it collects about the environmental state through social versus personal avenues or it might indicate the fidelity of social cues compared with information that an individual collects itself. Our formulation applies to those as well as any other cognitive, neurological or other mechanism that determines how individuals integrate separate sources of information.

It is worth highlighting an important but somewhat subtle property of our model: an individual's social samples are not simply additional independent random samples of the environmental state. Rather, an individual's social samples reflect personal samples that have already been collected by its social partners. This means that an individual's social assessment of the environment is based on shared information, namely, the observations that partners use for their own personal assessments. Moreover, the social assessments of different individuals may involve observation of the same social partner. In this case, those individuals' social samples will overlap and each will overlap with the shared partner's personal sample. This implies that personal and social samples are not independent and that personal, social and combined assessments will be correlated within the group. These interdependencies make deriving the value of social information for the 'average' individual far from straightforward. Below, we use both analytical and computational approaches to reveal the value of information, in terms of the accuracy with which the environmental state is assessed, gained from social sources compared to personal sampling of the environment. These 'returns' with respect to reduced ambiguity about the environment can ultimately be compared with the costs an individual pays for obtaining environmental information itself versus from its social partners.

ANALYSES AND RESULTS

Assessment Accuracy

The objective of this study is to understand how social information affects the accuracy of an individual's assessment of its environment. To that end, we compare an individual's personal

(e_{p_i}) and combined (e_i) assessments to the true value of the mean environmental state, μ, and measure accuracy as squared deviations (Fig. 1b). Specifically, the accuracy of individual i's personal assessment is

$$a_{p_i} = (e_{p_i} - \mu)^2 \tag{4}$$

and the accuracy of its combined assessment is

$$a_i = (e_i - \mu)^2 . \tag{5}$$

Note that smaller values of a_{p_i} and a_i indicate smaller errors and thus greater accuracy.

We measure the change in accuracy due to the addition of social information, Δa_i, as the difference

$$\Delta a_i = a_{p_i} - a_i . \tag{6}$$

The magnitude of Δa_i reflects the size of social information's impact on accuracy and its sign reveals the qualitative effect of social information on that individual's combined assessment: $\Delta a_i > 0$ indicates that social information improved accuracy compared to that individual's personal assessment and $\Delta a_i < 0$ indicates a reduction in accuracy. If an individual's social assessment is the same as its personal assessment, $\Delta a_i = 0$.

Expected Values

An individual's personal assessment, e_{p_i} is simply the average value of a random sample of size K from the environment (equation 1). Its expected value is $E(e_{p_i}) = \mu$, where μ is the environmental mean. The expected accuracy of this personal assessment, a_{p_i}, is

$$\overline{a}_p = E(a_{p_i}) = \frac{\sigma^2}{K} \tag{7}$$

where σ^2 is the environmental variance. Equation (7) follows from the fact that a_{p_i} is the squared deviation of assessment e_{p_i} from the mean μ (see equation 4) and so $\overline{a}_p$ is equivalent to the expected variance of a size-K sample mean (e.g. Casella & Berger, 2002; see Appendix for derivations). As is well known, the sample variance decreases with sample size. By the same token, the expected accuracy of an individual's personal assessment improves ($\overline{a}_p$ is reduced) with K.

The expected value of the combined assessment e_i (equation 3) is likewise $E(e_i) = \mu$. We have not found a general expression for the expected accuracy of the combined assessment, a_i (equation 5), but in the limit as N approaches infinity, this expectation is

$$\overline{a} = E(a_i) = \sigma^2 \left[\frac{(1-w)^2}{K} + \frac{w^2}{K_S} \right] , \tag{8}$$

where K_S is an individual's social sample size and w is the relative weight given to its social information (see equation 3 and the Appendix). From equations (7) and (8), it can be seen that the expected change in accuracy due to social sampling (equation 6) is, as N approaches infinity,

$$\overline{\Delta a} = E(\Delta a_i) = \frac{\sigma^2 w}{K} \left(2 - \frac{w}{\widehat{w}} \right) \tag{9}$$

where

$$\widehat{w} = \frac{K_S}{K + K_S} . \tag{10}$$

Our simulations (see below) show that equations (8–10) offer excellent approximations for groups of finite size, even groups with as few as $N = 3$ members. The right-hand side of equation (9) is positive – the combined assessment is more accurate – if $K_S > K$ or, if both $K_S \le K$ and $w \le 2\widehat{w}$. Expression (9) also reveals that social information is expected to reduce accuracy ($\overline{\Delta a} < 0$) if an individual's social information comprises fewer samples than its personal information ($K_S < K$) and that relatively depauperate social information is given too much emphasis ($w > 2\widehat{w}$) in its combined assessment. Whether social information improves or reduces accuracy, expression (9) shows that the magnitude of the change expected increases with the environmental variance, σ^2.

Effective Sample Size

Formulas (6) and (9) measure the impact of social information on an individual's environmental assessment in terms of change in squared deviations from the mean (see equations 4 and 5). It can be difficult to use this definition to interpret or compare impacts since, like the standard variance, their magnitude depends on the scale of measurement and it is expressed in squared units of measurement. To overcome these limitations, we develop a second, intuitive way to describe the information value of social sampling for individual assessments. The basic idea, explained below, is to quantify the value of social information in terms of the additional number of personal samples of the environment that the information would be equivalent to. That is, we express the information in terms of an 'effective sample size' (e.g. Faes, Molenberghs, Aerts, Verbeke, & Kenward, 2009).

We saw above (equation 7) that if an individual personally samples an environmental distribution with variance σ^2 a total of K times, then the expected accuracy is $\overline{a}_p = \sigma^2/K$. Rearranging this shows that the personal sample size can be expressed as $K = \sigma^2/\overline{a}_p$. Replacing $\overline{a}_p$ by the expected accuracy of the combined assessment, $\overline{a}$, in this expression defines the effective sample size, K_e:

$$K_e = \frac{\sigma^2}{\overline{a}} . \tag{11}$$

Expressed this way, K_e can be thought of as the size of a (hypothetical) personal random sample that would have the same accuracy as the combined assessments (cf. Faes et al., 2009). Since sample sizes are dimensionless and can be easily understood and compared, K_e represents an intuitive and more universal measure of the value of social information for an assessment.

An explicit formula for the effective sample size (equation 11) can be obtained by substituting the theoretical expectation for $\overline{a}$ (equation 8) into equation (11), giving

$$K_e = \left[\frac{(1-w)^2}{K} + \frac{w^2}{K_s} \right]^{-1} \tag{12}$$

in the limit as the group size N approaches infinity. Note that equation (12) does not depend on the environmental variance, σ^2. As a result, the value of social information described in terms of K_e will not depend on any measurement scale. Note too that application of the formula (12) would not require an estimate of the environmental variance.

A common-sense way to comprehend the value of an individual's social information is to make a comparison with its personal information about the environment. To that end, we compare an individual's social sample size K_S and effective sample size K_e to its personal sample size K. Letting $k_S = K_S/K$ and $k_e = K_e/K$

denote the relative values of the social and effective sample sizes, respectively, equation (12) can be rewritten more simply as

$$k_e = \frac{k_s}{w^2 + (1-w)^2 k_s} \ . \qquad (13)$$

Equation (13) shows that the relative effective sample size is determined completely by two parameters: w, the weight an individual places on its social information for the combined assessment, and by k_S, the relative size of the individual's social sample compared to its personal sample of the environment (Fig. 2).

It can be shown that k_e is maximized given a fixed k_S for the weight $\widehat{w}$ defined above (equation 10). The optimal weight itself can be expressed entirely in terms of k_S, $\widehat{w} = k_S/(1+k_S)$, and the corresponding effective sample size at this optimal weight is simply $\widehat{k}_e = k_S + 1$ (Fig. 2, dotted curve). $\widehat{k}_e$ sets an upper bound for the combined amount of information available for assessment for a fixed social sample of relative size k_S.

As noted above, small, overweighted social samples can degrade an individual's personal assessment of its environment. This can be understood more directly as a reduction in effective sample size compared to an individual's personal sample, $k_e < 1$, when $k_S < 1$ and $w > 2\widehat{w}$ (region above the white curve in Fig. 2). However social samples that are at least as large as personal ones (i.e. $k_S \geq 1$) ensure that $k_e \geq 1$ no matter how much or little an individual weighs its social information.

For any fixed value of w, equation (13) shows that k_e increases to the upper limit $(1-w)^{-2}$ as the relative size of the social sample k_S increases without bound (Fig. 3, dashed lines). If an individual gives social information a fixed emphasis w, its gains in assessment accuracy diminish after collecting $k_S = w/(1-w)$ social observations (indicated by the symbols in Fig. 3). If an individual favours its personal information over its social information ($w < 0.5$), this point of diminishing returns is below the personal sample size. It

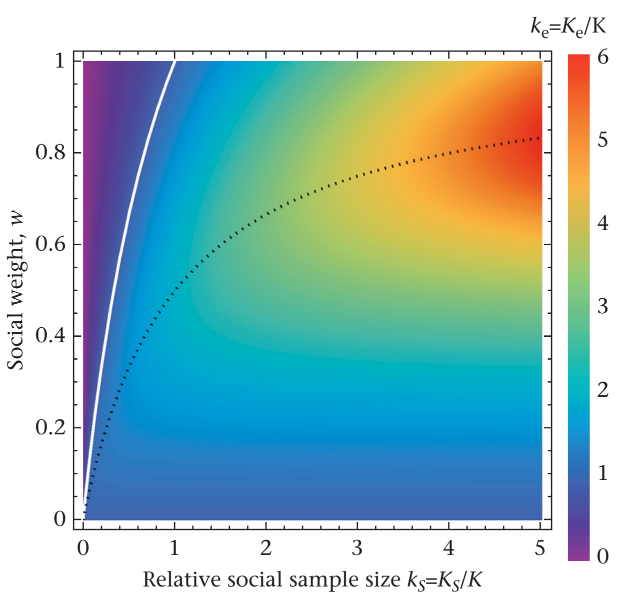

Figure 2. Relative effective sample size $k_e = K_e/K$, the size of an individual's effective sample relative to the size of its personal sample, as function of the weight w given to social information and relative social sample size $k_S = K_S/K$, the size of an individual's social sample relative to the size of its personal sample (equation 13). Dotted curve shows where k_e is maximized given k_S, at the optimal weight $\widehat{w}$ (equation 10). White curve shows the contour for $k_e = 1$; that is, combinations of k_S and w for which the effective sample size is equal to the personal sample size; combinations of w and k_S above this curve are cases where social information reduces the accuracy provided by personal sampling.

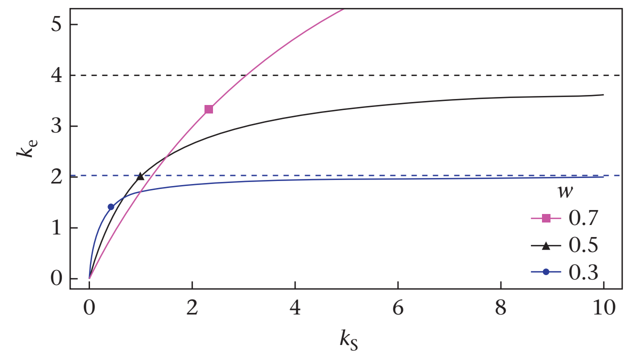

Figure 3. Relative effective sample size $k_e = K_e/K$, the size of an individual's effective sample relative to the size of its personal sample, as a function of relative social sample size $k_S = K_S/K$, the size an individual's social sample relative to the size of its personal sample for social weightings $w = 0.3$ (solid blue line with circle), $w = 0.5$ (solid black line with triangle) and $w = 0.7$ (solid magenta line with square). Symbols are located at the point of diminishing returns for each curve. Dashed lines indicate the asymptotic maximum values of k_e as k_S approaches infinity, $(1-w)^{-2}$, for the cases $w = 0.3$ and $w = 0.5$ (not shown for $w = 0.7$).

may be possible to use these theoretical limits to estimate w experimentally, by comparing the accuracies of individuals with no social information either (1) to those saturated with social information, the ratio of which should equal $(1-w)^2$, or (2) to the social sample size at which accuracy increases begin to slow, the ratio of which is predicted by $(1-w)/w$.

Simulations for Finite-sized Groups

The model and results described thus far make several simplifying assumptions that might conceivably affect the impact of social information on individual assessments. First, the environmental distribution is described only by its mean state μ and variance σ^2. However, other aspects of the environment, such as whether it varies discretely or continuously, may influence assessments. Second, the social sample in our model may be based on structured subsets of social partners (e.g. single observations each from many partners or a composite observation from a single partner). Lastly, our analytical solutions represent expectations for infinitely large group sizes. However, in many species and contexts, the group size (N) from which individuals can sample socially may be quite small. This could conceivably influence our results because assessments of group members may be strongly correlated in small groups. We used computer simulations coded in R (R Core Team, 2020) to explore consequences of violating these assumptions by considering different types of environmental variation, finite group sizes and a spectrum of social sampling methods.

First, we compared assessments of discrete versus continuous environmental variation. In our simulations, we used a Bernoulli distribution to model dichotomous variation, with parameter ε equal to the probability of encountering (or the fraction of) one state (e.g. 'present' or 'large'); the alternative state ('absent' or 'small') occurs with probability $1-\varepsilon$. If one assigns the value 1 to the first state and 0 to the second, the mean environmental state that each individual seeks to assess is $\mu = \varepsilon$. The corresponding variance is $\sigma^2 = \varepsilon(1-\varepsilon)$, which is maximized when $\varepsilon = 0.5$. Note that the mean and variance both depend on ε. For continuous variation, we used a normal distribution with mean μ and variance σ^2. Unlike the Bernoulli distribution, the mean and variance for the normal distribution are distinct parameters. Despite their differences, our simulations revealed almost identical results for the two distributions. In particular, simulation results (Fig. 4) showed the same change in accuracy due to social information across the range of σ^2 values whether the environmental state was a dichotomous, Bernoulli random variable or continuous with a normal distribution. These results also matched our theoretical expectations (equations 7–10; Fig. 4, black lines), which suggests that our formulas apply equally well to assessments of discrete and continuous environmental variation.

The formulas for the expected combined assessment $\overline{a}$ (equation 8), the expected change in accuracy $\overline{\Delta a}$ (equation 9), and the effective and relative effective sample sizes K_e and k_e (equations 12 and 13) are exact only for a group of infinite size N. To examine their validity for finite-sized groups, for each set of given parameters (Table 1) and group size N, we simulated replicate groups, recording the members' personal and combined assessments (equations 2 and 3) and accuracies (equations 4–6) for each replicate. We compared the averages of the replicate finite-N groups to our analytical expectations for infinitely sized groups across a broad range of parameter values. A representative summary of our simulation results is given in the Appendix (Table A1), and the R code used to obtain them can be found in the Supplementary Materials (see also Figs 4–6).

It was unclear a priori what impact small group size might have on the group average value of social information in our model. Consider, for example, the extreme case of a group with $N = 2$ individuals each with personal sample size $K = 1$. Since the two members can socially observe only each other's single personal sample, it is necessarily the case that $e_{s_1} = e_{p_2}$ and $e_{s_2} = e_{p_1}$. That is, the social sample of one is the personal sample of the other and vice versa. The correlation between their combined assessments (equation 3) is $2w\,(1-w)/[\,(1-w)^2 + w^2]$, which is perfect if $w = 0.5$ (see Appendix for the derivation). For groups with more than two members, the social information observed by different individuals may also overlap (e.g. two individuals observe the same third group member). This should contribute to positive correlations among members' social assessments e_{s_i} (equation 2) and, thus, among their combined assessments. These sources of overlap should, in principle, reduce the amount of social information extracted by the group as a whole for assessment. However, in the limit as N goes to infinity, the probability of shared information is negligible and social information obtained by different individuals is uncorrelated.

Our simulations considered a range of finite group sizes N from 3 to 100 (see Appendix, Table A1). In all cases we examined, the cross-replicate average of $\langle \Delta a \rangle$ – the group-mean change in accuracy, which can also be interpreted as the change in accuracy of an average member of the group – was nearly the same as the infinite-group expectation $\overline{\Delta a}$ (equation 9; see, e.g. the red arrow in Fig. 5). The results revealed that group size has a direct impact on the degree of variation among replicates in the group-average change $\langle \Delta a \rangle$, namely, there is more variation in smaller groups than in larger groups (compare the teal and pink histograms in Fig. 5 and see Appendix, Table A1). While perhaps not surprising when viewed in the context of the law of large numbers (e.g. Casella & Berger, 2002), this finding implies that the average member of a smaller group has a greater chance of experiencing reduced accuracy using social information than the average member of a larger group (regions where $\langle \Delta a \rangle < 0$; left of the dashed line in Fig. 5) for the same combination of parameter values.

Formula (8) shows that the expected accuracy of the combined assessment depends on K_S, the total number of social samples obtained from social partners. However, this analytical result does not consider the manner in which social information is acquired. We used our simulations to explore a spectrum of scenarios by which an individual could obtain its K_S social observations: sample one observation from each of K_S social partners, sample K_S observations from a single social partner, or sample K_S observations from among all $(N-1)K$ observations obtained by social partners in a group of size N with personal sample size K. Our simulations indicated that these dramatically different sampling scenarios had minimal

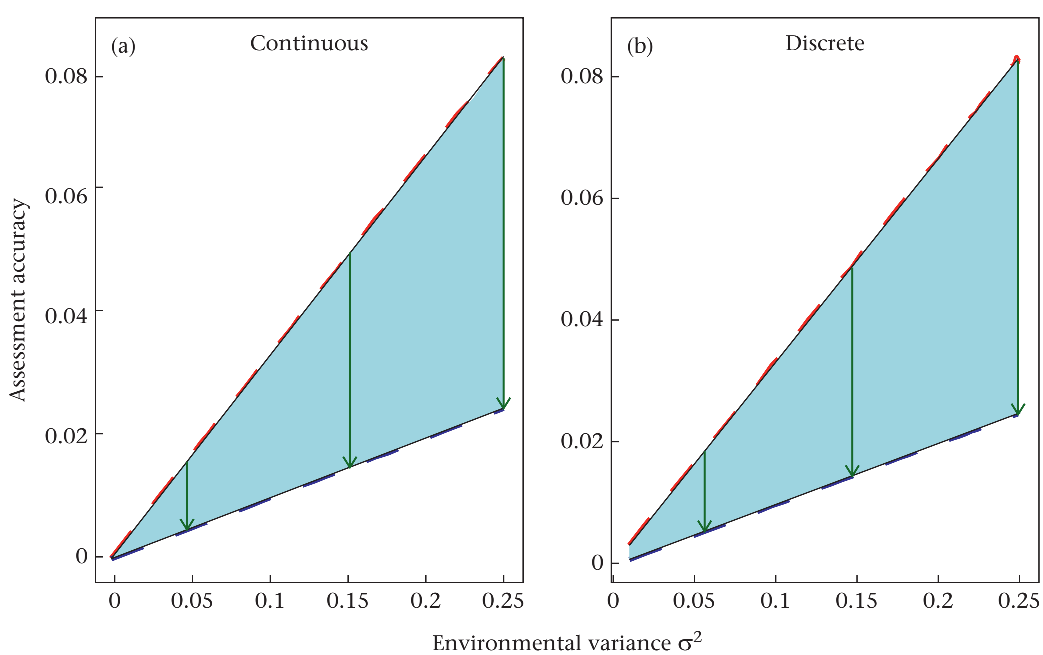

Figure 4. Simulations of (a) continuous and (b) discrete environments showing effects of environmental variance (σ^2) on the average accuracies across replicates of personal (a_{p_i}, upper red dashed lines, equation 4) and combined (a_i, lower blue dashed line) assessments of the mean environmental state μ. Smaller values for accuracy indicate assessments that are closer to the true mean environmental state. Green arrows show the effect of social information on assessment (Δa_i; equation 6) for three arbitrarily chosen values of σ^2; downward arrows indicate improved accuracy. (a) Normally distributed environment with mean $\mu = 0$, variance σ^2. (b) Dichotomous environment with parameter ε; the mean $\mu = \varepsilon$ and variance $\sigma^2 = \varepsilon(1 - \varepsilon)$. Theoretical expectations are indicated for the combined (lower black lines; equation 8) and private (upper black lines; equation 7) assessments. Simulations are based on 10 000 replicates of each parameter set, $N = 20$, social weighting $w = 0.50$, personal sample size $K = 3$, and social sample size $K_S = 5$.

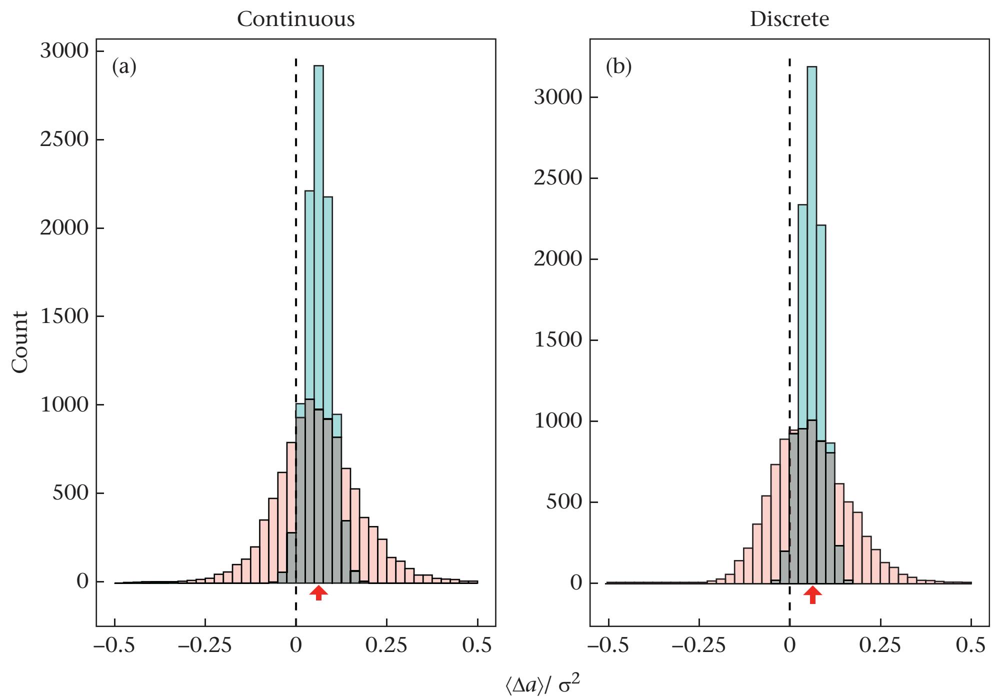

Figure 5. Effect of group size N on the distribution of group-average changes in accuracy due to social information, $\langle\Delta a\rangle$, scaled by σ^2, the environmental variance over 10 000 replicate groups. Teal and pink histograms show results for $N = 100$ (teal bars) and $N = 10$ (pink bars), respectively. Values of $\langle\Delta a\rangle/\sigma^2$ left of the dashed line indicate group-average reductions in accuracy. The red arrow indicates the expected change in accuracy given by equation (9). Simulations based on parameter combinations with personal sample size $K = 4$, social sample size $K_S = 2$, and social weighting $w = 0.5$. (a) Normally distributed environment with mean $\mu = 0$, variance σ^2; theoretical expectation (equation 9): 0.0625; distribution averages: 0.0629 ($N = 10$), 0.0630 ($N = 100$). (b) Dichotomous environment with parameter ε; the mean $\mu = \varepsilon$, variance $\sigma^2 = \varepsilon\,(1 - \varepsilon)$; theoretical expectation: 0.0625; distribution averages: 0.0630 ($N = 10$), 0.0624 ($N = 100$).

effects on the mean over replicates of $\langle\Delta a\rangle$, the group-average change in accuracy; this mean was always close to the large group expectation $\overline{\Delta a}$ (equation 9).

The simulation results showed that the distributions of the group-average changes were also largely similar across sampling scenarios, except that variance in $\langle\Delta a\rangle$ among replicates was lowest

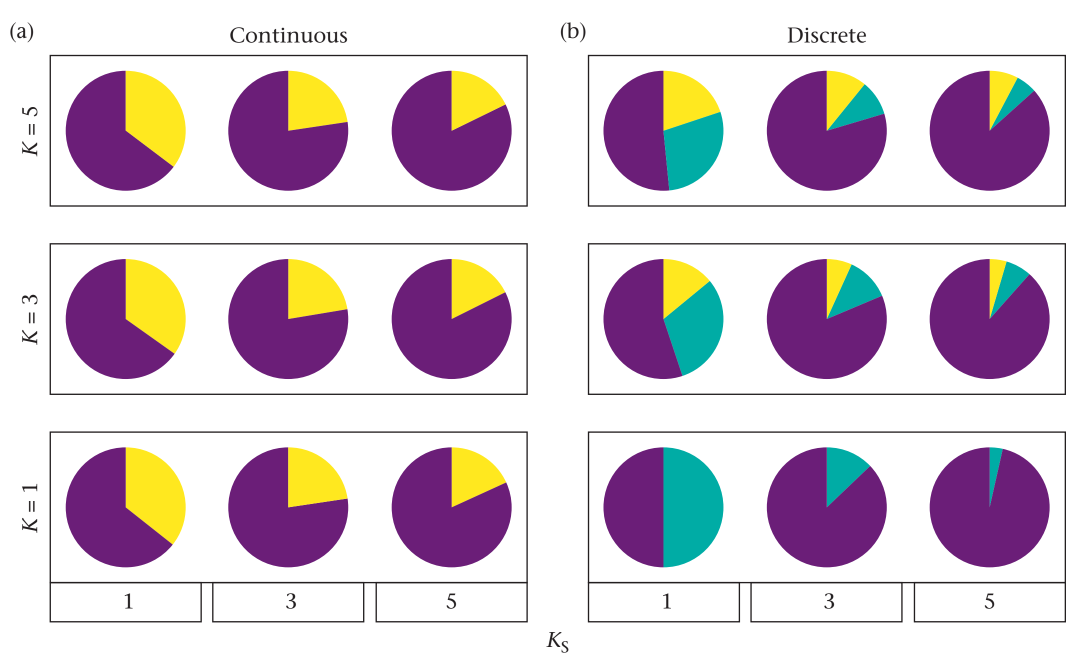

Figure 6. Proportion of individuals that increased (purple), decreased (yellow) or showed no change (green) in accuracy for different combinations of personal (K) and social information (K_S) for group size $N = 100$, and weight $w = 0.50$. Simulations based on 10 000 replicates. (a) Normally distributed environment with mean $\mu = 0$, variance σ^2. (b) Dichotomous environment with parameter ε; the mean $\mu = \varepsilon$ and variance $\sigma^2 = \varepsilon(1 - \varepsilon)$.

when an individual takes its K_S social observations from a single or small subset of partners randomly selected from the group, each with a personal sample size of K (see Appendix, Table A1). The ratio between the variances for widely versus narrowly sampled social observations approached $(K_S-1)K{:}1$ as social information is weighted more heavily. We did not pursue this curiosity further but suspect an explanation could be found via the theory of one-way random effects analysis of variance (Scheffé, 1959) by thinking abstractly of the social partners each individual observes as random effects.

Our simulations allowed us to examine not just the average, $\langle \Delta a \rangle$, but the entire distribution of assessment changes (equation 6) within a group. The results showed that, overall, the proportion of individuals whose accuracy is improved by social information increased with K_S (Fig. 6). We also found that even when social information is expected to improve accuracy for the average member ($\overline{\Delta a} > 0$; equation 9), social sampling can nevertheless degrade environmental assessments for a fraction of the group (Fig. 6).

DISCUSSION

Our goal was to develop well-founded insights into how social information might affect an individual's ability to assess its environment. To that end, we used a modelling approach that allowed us to measure the impact of social information on assessment, completely separate from the individual's decision-making process. We derived general formulas that describe in mathematical terms the expected influences of personal and social sampling efforts, and how individuals combine these sources of information to appraise their environment. We also explored potential ramifications of group size, social sampling practices and environment type.

We found that when incorporating social information, the expected change in accuracy of assessments, for better or worse, was greater in more variable environments than in less variable ones. These results are consistent with other theoretical models predicting that individuals should favour social information when an environment is uncertain (Boyd & Richerson, 1988; Kameda & Nakanishi, 2002; Smolla, Alem, Chittka, & Shultz, 2016; Stephens, 1989). Moreover, empirical work manipulating the degree of environmental uncertainty has found that animals tend to favour social information under more uncertain conditions. For example, when uncertainty about the palatability of food items was increased experimentally, rats relied more heavily on social information than on personal experience in foraging decisions (Galef, 2009). Similarly, when cues that once provided reliable information about profitable foraging patches no longer reflected the presence of food, individuals tended to rely more on social information from conspecific demonstrators (Baciadonna, McElligott, & Briefer, 2013). Thus, our findings add to a growing body of work indicating that social information can be particularly important when conditions are highly variable.

Our findings also highlight that the impact of social information on the accuracy of environmental assessments depends on how heavily that information is weighted by individuals. Our model reveals that social information leads to more severe inaccuracies when sparse social information is given too much weight by the individual. More generally, the emphasis an individual gives its social information determines not just whether it improves its ability to assess a given environment but also the magnitude of improvement or degradation. Our results indicate that there is an optimal weighting that allows for maximum accuracy based on the amounts of social and personal information an individual can access; higher and lower weights from this optimal value yield less accuracy for the same information.

Many theoretical models of decision making have assumed that animals weigh personal and social information equally. Early work on group foraging assumed that animals use personal information and information from others to the same degree while assessing the distribution of food resources within an environment (Clark & Mangel, 1984; Templeton & Giraldeau, 1996; Valone, 1989). However, empirical evidence now suggests that animals may weigh different sources of information unequally (Baciadonna et al., 2013; Coolen et al., 2005; Galef, 2009; Grüter, Czaczkes, & Ratnieks, 2011; Webster & Laland, 2018). These empirical studies have examined how factors such as past experience, costs of personal sampling, and conflicting information influence the weighting of social information. It would be interesting to reinterpret these differential uses of information in light of our new results.

To the extent that higher accuracy improves fitness (Koops, 2004; Koops & Abrahams, 1998), individuals that make suboptimal assessments should be selectively culled from the population over time, leaving only those who use optimal weightings in contemporary populations. However, individual weightings that evolved in response to ancestral conditions might become maladaptive in populations experiencing, say, a precipitous drop in abundance, potentially affecting the availability of social information. In that case, a particular weighting of social information that may have been beneficial when it was abundant could prove costly were it suddenly to become scarce. Such a scenario assumes weighting of social information is fixed. However, individuals may be able to adjust their weighting in a context-dependent manner (e.g. the weight given to social information might depend on group size). Several empirical studies suggest that, at least in some cases, animals can flexibly adjust the weight placed upon social information (Baciadonna et al., 2013; Coolen et al., 2005; Galef, 2009). Still, more theoretical and empirical work will be needed to understand the mechanisms and consequences of flexible weighting.

Our results also show that the benefits of social information to assessment accuracy should be bounded by an upper limit that is determined by the relative weight an individual gives that information. We speculate that this theoretical upper bound might serve as a conduit for estimating those weights empirically, either by experimentally saturating an individual with social information or using manipulations to reveal a point of diminishing returns for an individual of additional social versus personal observations of the environment.

The results of our simulations suggest that group size influences the impact of social information on assessment accuracy. Although the change in accuracy does not differ with group size on average, the variation of this change realized among group members was higher in smaller groups. This means that, all else being equal, individuals are more likely to be misled (i.e. reduce accuracy) by using social information as group size declines. Using a different theoretical framework, King and Cowlishaw (2007) demonstrated that when personal information is accurate, animals in groups should share information and that the benefits of social information use increase with group size. Pooling information in this way, especially in larger groups, can allow individuals to make accurate behavioural decisions regardless of the accuracy of their personal information. Moreover, empirical work with fish suggests that improved predator avoidance in larger groups results from social information use (Ward, Herbert-Read, Sumpter, & Krause, 2011). These results are complementary to our prediction that social information is less likely to erode accuracy in large groups compared to smaller ones. Further research is needed to determine whether those findings share a common foundation with ours.

We found that the means by which individuals gather social information, whether collected from just one or multiple social partners, had little influence on the quality of their environmental assessments. If social sampling approaches differ in their costs of implementation, then we should expect to find all individuals using the least costly approach available. Factors such as cognitive abilities and distribution of conspecifics across the landscape could contribute to the information collection approaches available and their costs. An additional aspect of the sampling approach that we did not examine in our model is the temporal pattern of sampling. It has been shown that the temporal order in which individuals observe social partners can have a significant impact on the quality of information gathered by different group members above and beyond just the total number of social observations (Mann, 2018).

Our main findings are valid for both discrete and continuous environmental variation and thus should be widely applicable to a broad range of local habitat variables that animals might assess. We note, however, that our analyses assume individuals are evaluating the mean state of the environment. While this is reasonable in many situations, animals might also benefit from assessments of other environmental properties, such as its overall level of variability or the likelihood of a particularly extreme state such as drought or lethal temperatures. For example, animals are known to adjust behaviour based on the degree of uncertainty about predation risk (Kruschel & Schultz, 2011; Polo, López, & Martín, 2011).

Adaptive responses to environmental variation require that organisms accurately assess their surroundings. In animals, it seems reasonable to conjecture that information obtained from social partners may be a particularly cost-efficient means of reducing ambiguity, but it has been difficult to evaluate this proposition since assessments and their consequences are confounded in most studies of behaviour. The theoretical approach we used allowed us to isolate the assessment process and evaluate how social information can affect it. Our findings suggest that social information may improve or worsen animals' assessments, and we also predict the conditions under which those outcomes would be expected. A full understanding of adaptive environment-dependent behaviour will eventually require stitching our results to those concerned with costs of information gathering, individual decision making and the consequences for survival and reproduction. Until then, this study highlights why correctly accounting for assessment, apart from behaviours and their consequences, contributes to a more profound understanding of how the complex process of decision making in animals can shape and be shaped by its adaptive evolution.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2021.06.009.

APPENDIX: DERIVATIONS OF ANALYTICAL EXPRESSIONS

An individual's personal assessment e_{p_i} (equation 1) is the average of a random sample of size K from the environmental distribution, which has mean μ and variance σ^2. Because the samples are independent and identically distributed, the expected value of this sample average is

$$E(e_{p_i}) = E\left(\frac{1}{K}\sum_{j=1}^{K} X_{ij}\right) = \frac{1}{K}\sum_{j=1}^{K} E(X_{ij}) = \frac{1}{K}\sum_{j=1}^{K}\mu = \frac{K\mu}{K} = \mu \quad \text{(A1)}$$

and the variance is

$$V(e_{p_i}) = V\left(\frac{1}{K}\sum_{j=1}^{K} X_{ij}\right) = \sum_{j=1}^{K}\frac{V(X_{ij})}{K^2} = \sum_{j=1}^{K}\frac{\sigma^2}{K^2} = \frac{\sigma^2}{K}\ . \quad \text{(A2)}$$

The second equality in equation (A2) follows from the assumption that samples are independent. Note that the expected value of the personal accuracy measure is

$$E(a_{p_i}) = E(e_{p_i} - \mu)^2 = V(e_{p_i}) = \frac{\sigma^2}{K}. \quad \text{(A3)}$$

Similarly, for the social assessments,

$$E(e_{s_i}) = E\left(\frac{1}{K_s}\sum_{j=1}^{K_s} Y_{ij}\right) = \frac{1}{K_s}\sum_{j=1}^{K_s} E(Y_{ij}) = \frac{1}{K_s}\sum_{j=1}^{K_s}\mu = \frac{K_s\mu}{K_s} = \mu \quad \text{(A4)}$$

The expected value of the combined assessment (equation 3) is

$$E(e_i) = E\left[(1-w)e_{p_i} + we_{s_i}\right] = (1-w)\mu + w\mu = \mu\ . \quad \text{(A5)}$$

Since the personal and social samples are gathered independently, this gives the variance

$$V(e_i) = (1-w)^2\frac{\sigma^2}{K} + w^2\frac{\sigma^2}{K_s} = \sigma^2\left[\frac{(1-w)^2}{K} + \frac{w^2}{K_s}\right]. \quad \text{(A6)}$$

Equation (8) follows from this because $\bar{a} = E(a_i) = E(e_i - \mu)^2 = V(e_i)$.

The maximum value of the relative effective sample size k_e given k_S (equation 13) can be found by setting the derivative of k_e with respect to w,

$$\frac{dk_e}{dw} = \frac{2k_S[k_S - w(1+k_S)]}{\left[w^2 + (1-w)^2 k_S\right]^2}\ , \quad \text{(A7)}$$

equal to zero and solving for w. The solution is $\hat{w} = k_S/(1+k_S)$, which, substituted in equation (13) and simplifying shows that $\hat{k}_e = k_S + 1$.

In a group of size $N = 2$ where each individual obtains a single personal sample ($K = 1$), the covariance between the combined assessments (equation 3) of the members is

$$\mathrm{Cov}(e_1,\ e_2) = \mathrm{Cov}\left[(1-w)e_{p_1} + we_{s_1}, (1-w)e_{p_2} + we_{s_2}\right] = (1-w)^2\mathrm{Cov}(e_{p_1}, e_{p_2}) + w(1-w)\left[\mathrm{Cov}(e_{p_1}, e_{s_2}) + \mathrm{Cov}(e_{p_2}, e_{s_1})\right] + w^2\mathrm{Cov}(e_{s_1}, e_{s_2}) \quad \text{(A8)}$$

In this extreme case, $e_{s_1} = e_{p_2}$ and $e_{s_2} = e_{p_1}$, so equation (A8) is equivalent to

$$\mathrm{Cov}(e_1, e_2) = \left[(1-w)^2 + w^2\right]\mathrm{Cov}(e_{p_1}, e_{p_2}) + w(1-w)\left[\mathrm{Cov}(e_{p_1}, e_{p_1}) + \mathrm{Cov}(e_{p_2}, e_{p_2})\right] = 2w(1-w)\sigma^2 \quad \text{(A9)}$$

where the second equation follows from $\mathrm{Cov}(e_{p_1}, e_{p_2}) = 0$ (personal samples are independent) and $\mathrm{Cov}(e_{p_i}, e_{p_i}) = V(e_{p_i}) = \sigma^2$ for $i = 1, 2$ (equation A2 with $K = 1$). Combining equation (A9) with equation (A6) shows that the correlation between the combined assessments is

$$\mathrm{Corr}(e_1, e_2) = \frac{\mathrm{Cov}(e_1, e_2)}{\sqrt{V(e_1)V(e_2)}} = \frac{2w(1-w)\sigma^2}{\left[(1-w)^2 + w^2\right]\sigma^2} = \frac{2w(1-w)}{(1-w)^2 + w^2}. \tag{A10}$$

Table A1
Representative selection of simulation results for finite groups and social sampling methods

Method	$N = 3$	$N = 10$	$N = 100$	$N = 3$	$N = 10$	$N = 100$
	$K = 2, K_S = 2$			**$K = 4, K_S = 2$**		
$w = 0.25$						
Unstructured[1]	0.04539	0.01249	0.00120	0.01475	0.00408	0.00039
Dispersed[2]	0.04831	0.01240	0.00119	0.01597	0.00428	0.00040
Integrated[3]	0.04379	0.01102	0.00107	0.01057	0.00284	0.00027
$w = 0.5$						
Unstructured	0.09967	0.03175	0.00297	0.03798	0.01580	0.00116
Dispersed	0.11917	0.03061	0.00294	0.04470	0.01201	0.00119
Integrated	0.07757	0.02231	0.00218	0.01992	0.00545	0.00055
$w = 0.75$						
Unstructured	0.12655	0.04274	0.00445	0.07569	0.02557	0.00258
Dispersed	0.15657	0.04721	0.00451	0.08724	0.02639	0.00258
Integrated	0.07187	0.02427	0.00266	0.01756	0.00635	0.00066
	$K = 3, K_S = 2$			**$K = 2, K_S = 4$**		
$w = 0.25$						
Unstructured	0.02323	0.00631	0.00063	0.04077	0.01089	0.00107
Dispersed	0.02304	0.00652	0.00063	0.03498	0.01047	0.00102
Integrated	0.01758	0.00474	0.00048	0.01019	0.00275	0.00028
$w = 0.5$						
Unstructured	0.05719	0.01675	0.00168	0.09876	0.02763	0.00277
Dispersed	0.06028	0.01687	0.00169	0.09466	0.02968	0.00274
Integrated	0.03503	0.00988	0.00098	0.01840	0.00563	0.00056
$w = 0.75$						
Unstructured	0.08879	0.03095	0.00309	0.10853	0.03917	0.00392
Dispersed	0.10909	0.03145	0.00308	0.12985	0.04051	0.00396
Integrated	0.03070	0.01115	0.00116	0.01645	0.00611	0.00066

Entries indicate the variance among 10 000 replicates of $\langle \Delta a \rangle$, the group-mean change in accuracy, for the given personal sample size K, social sample size K_S, social weighting w, group size N and social sampling method. In all cases, the mean over replicates of Δa matched the infinite group size expectation (equation 9); this expectation is positive for all cases except $K = 4$, $K_S = 2$, $w = 0.75$. Simulations all assumed environmental mean $\mu = 0$ and variance $\sigma^2 = 1$.

[1] K_S social samples selected at random without replacement from all $N \times K$ observations.

[2] Social samples obtained by selecting one observation from K_S different, randomly selected social partners.

[3] K_S social samples obtained from M randomly selected social partners, where M is the smallest integer greater than or equal to K_S/K.