



CrossMark
click for updates

Research

Cite this article: Wolf M, Kurvers RHJM, Ward AJW, Krause S, Krause J. 2013 Accurate decisions in an uncertain world: collective cognition increases true positives while decreasing false positives. *Proc R Soc B* 280: 20122777.
<http://dx.doi.org/10.1098/rspb.2012.2777>

Received: 22 November 2012

Accepted: 17 January 2013

Subject Areas:

behaviour, cognition, ecology

Keywords:

collective intelligence, swarm intelligence, decision accuracy, group-decision-making, collective behaviour, anti-predation

Author for correspondence:

Max Wolf

e-mail: m.wolf@igb-berlin.de

[†]These authors contributed equally to this study.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2012.2777> or via <http://rspb.royalsocietypublishing.org>.

Accurate decisions in an uncertain world: collective cognition increases true positives while decreasing false positives

Max Wolf^{1,†}, Ralf H. J. M. Kurvers^{1,†}, Ashley J. W. Ward^{1,2}, Stefan Krause³ and Jens Krause¹

¹Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Mueggelseedamm 310, 12587 Berlin, Germany

²School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia

³Department of Electrical Engineering and Computer Science, Lübeck University of Applied Sciences, 23562 Lübeck, Germany

In a wide range of contexts, including predator avoidance, medical decision-making and security screening, decision accuracy is fundamentally constrained by the trade-off between true and false positives. Increased true positives are possible only at the cost of increased false positives; conversely, decreased false positives are associated with decreased true positives. We use an integrated theoretical and experimental approach to show that a group of decision-makers can overcome this basic limitation. Using a mathematical model, we show that a simple quorum decision rule enables individuals in groups to simultaneously increase true positives and decrease false positives. The results from a predator-detection experiment that we performed with humans are in line with these predictions: (i) after observing the choices of the other group members, individuals both increase true positives and decrease false positives, (ii) this effect gets stronger as group size increases, (iii) individuals use a quorum threshold set between the average true- and false-positive rates of the other group members, and (iv) individuals adjust their quorum adaptively to the performance of the group. Our results have broad implications for our understanding of the ecology and evolution of group-living animals and lend themselves for applications in the human domain such as the design of improved screening methods in medical, forensic, security and business applications.

1. Introduction

Decision-makers in a wide range of contexts, including predator avoidance, medical decision-making, job candidate selection and security screening, face a fundamental dilemma [1–9]. The goal of the decision-maker is to take an action whenever a particular condition in its environment is fulfilled but not to take this action when the condition is not fulfilled. Animals, for example, aim to run away in the presence of predators but not in their absence, doctors aim to provide a treatment when a disease is present but not when it is absent. Whether or not the condition in question is fulfilled is unknown to the decision-maker at the point in time when the decision must be made and has to be inferred from cues. These cues, however, are seldom perfectly correlated with the condition: cues that are indicative for a certain condition (e.g. presence of predator/disease) may be present in the absence of that condition, conversely, cues may be absent in the presence of that condition. By increasing responsiveness to such cues, decision-makers thus increase not only their chance of correctly taking the action in the presence of the condition (e.g. run away in the presence of predators, provide treatment in the presence of the disease) but also that of erroneously taking this action in its absence (e.g. run away in the absence of predators, provide treatment in the absence of the disease). Increased true positives (a.k.a. hits in detection theory) are thus associated with increased false positives (a.k.a. false alarms in detection theory), giving rise to a fundamental limitation of decision accuracy

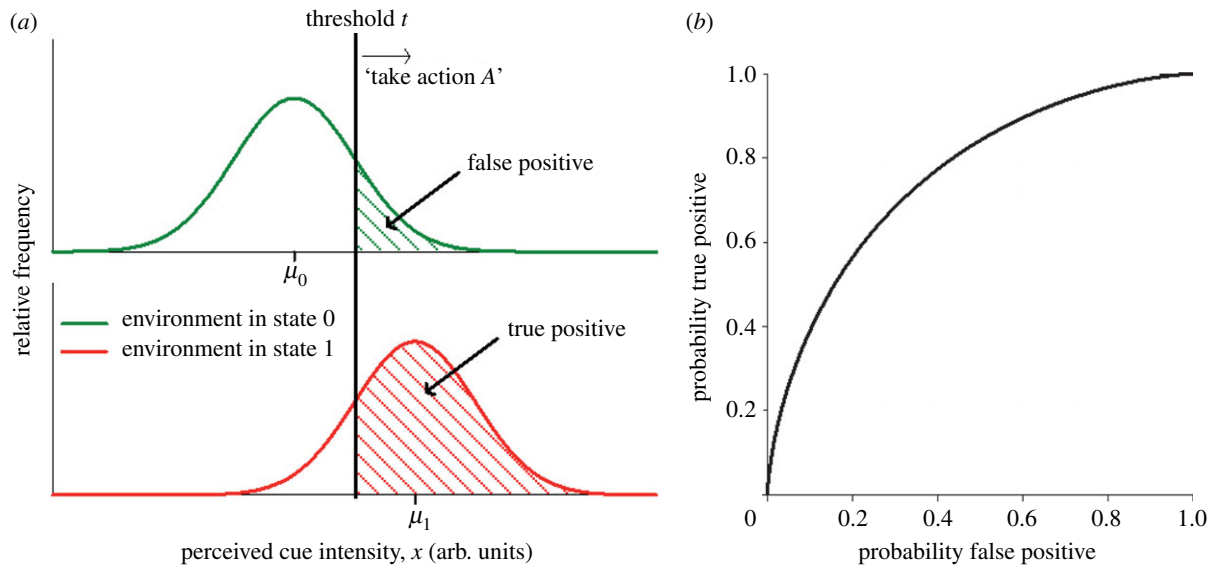


Figure 1. Generic decision-making context illustrating that a solitary decision-maker can increase true positives only at the cost of increased false positives. The decision-maker has to decide whether or not to take an action *A*. Whether or not he/she should take this action depends on the environment which can be in either of two states. If the environment is in state 0 the decision-maker should not take the action, if it is in state 1 he/she should take the action. While the decision-maker does not observe the state of the environment, he/she perceives a cue of intensity *x* which provides some information about the state of the environment. (a) The cue *x* is drawn from a normal distribution $X \sim \mathcal{N}(\mu_i, \sigma^2)$ where the mean μ_i of that distribution depends on the state of the environment. Independent of the payoffs associated with behavioural decisions, it will be optimal to use a threshold rule 'do not take action *A* when $x \leq t$, take action *A* when $x > t$ ' (assuming $\mu_0 < \mu_1$). Both true positives (i.e. take action *A* in state 1) and false positives (i.e. take action *A* in state 0) are strictly decreasing functions of the threshold *t*. Consequently, by increasing the threshold *t*, individuals simultaneously decrease the probability of taking the action in state 0 and state 1, resulting in the well known trade-off between true and false positives (b) that decision-makers face. The black line in (b) indicates the combinations of true and false positives that the decision-maker can achieve by varying *t* for the particular case of $\mu_0 = -1$, $\mu_1 = 1$ and $\sigma = 2$.

Table 1. Five examples that fit the scenario depicted in figure 1.

decision-maker	environment		action		cues available to decision-maker (examples)
	state 0	state 1	false positive	true positive	
animal under predation risk	predator absent	predator present	run away when predator absent	run away when predator present	visual, auditory and olfactory stimuli
doctor	disease absent	disease present	provide treatment when disease absent	provide treatment when disease present	patient-reported symptoms, physical examination, medical images (e.g. X-rays, MRI)
search committee (e.g. job search, university admission)	candidate unsuitable	candidate suitable	hire/ admit unsuitable candidate	hire/ admit suitable candidate	CV, reference letters, interview, test scores
psychiatrist/clinical psychologist	patient harmless	patient dangerous	classify harmless patient as dangerous	classify dangerous patient as dangerous	information about past actions of person, patient self-reports, reports by third parties
security personnel	person harmless	person dangerous	take preventive actions when harmless	take preventive actions when dangerous	information about past actions of person, visual observations

under uncertainty [2,6,10,11]. Figure 1 illustrates this dilemma for a simple but generic decision-making context under uncertainty; table 1 summarizes five examples that fit this scenario.

Decision accuracy under uncertainty is thus fundamentally constrained by the trade-off between true and false positives. A high rate of true positives is possible only at the cost of a

high rate of false positives; conversely, a low rate of false positives is possible only at the cost of a low rate of true positives. We here use an integrated theoretical and experimental approach to show that a group of decision-makers using a simple quorum decision rule can overcome this basic limitation: compared with a solitary decision-maker, a group of decision-makers can both increase true positives and decrease false positives simultaneously.

We proceed in two steps. First, we show mathematically that, compared with solitary decision-makers, a simple quorum decision rule allows decision-makers in groups to increase true positives and decrease false positives simultaneously. In particular, this effect is achieved whenever decision-makers use a quorum threshold that is set above the false-positive rate and below the true-positive rate of solitary decision-makers. Second, we present results from experiments that we conducted on humans that are consistent with our model predictions: (i) after observing the choices of the other group members, individuals both increase true positives and decrease false positives, (ii) this effect gets stronger as group size increases, (iii) individuals use a quorum threshold set between the average true and false-positive rates of the other group members, and (iv) individuals adjust their quorum adaptively to the performance of the group.

2. Mathematical analysis and predictions

Consider a group of N decision-makers that face a situation as depicted in figure 1 and assume that each of those decision-makers balances the trade-off between true and false positives such that he/she commits true and false positives with probabilities $p_{\text{true}+}$ and $p_{\text{false}+}$, respectively. Assume that each decision-maker uses the following two-step decision rule: ‘indicate to take action A whenever your personal information indicates that you should take action A (i.e. whenever the perceived cue intensity x exceeds the decision threshold t , figure 1), take action A when at least a fraction q of the other group members indicate to take action A ’. Figure 2 illustrates the consequences of this rule for a particular example with $p_{\text{true}+} = 0.6$ (red hatched lines) and $p_{\text{false}+} = 0.3$ (green hatched lines) for the three cases of a low (figure 2a), a high (figure 2b) and an intermediate (figure 2c) quorum threshold q . When using a low or a high quorum threshold, decision-makers in groups cannot overcome the trade-off between true and false positives that solitary decision-makers face. For low thresholds (figure 2a, $q = 0.1$), increasing group size gives rise to increased true positives (red dots), but these increases are associated with increased false positives (green dots). Similarly, for high thresholds (figure 2b, $q = 0.8$), increasing group size gives rise to decreased false positives, but these decreases are associated with decreased true positives. A very different scenario occurs, however, for intermediate thresholds (figure 2c, $q = 0.45$), where increasing group size is associated with increased true positives and decreased false positives simultaneously. Hence, when using intermediate thresholds (i.e. thresholds below the true-positive $p_{\text{true}+}$ and above the false positive $p_{\text{false}+}$, see below), decision-makers in groups can overcome the trade-off between true and false positives that solitary decision-makers face. In fact, even for relatively small group sizes (≈ 20), this mechanism allows decision-makers in groups to achieve a very good match between

their behaviour and the true state of the environment (e.g. run when a predator is present and stay when a predator is absent; provide treatment when disease present, do not provide treatment when disease absent).

How can this result be understood? Above, we assumed that, given the state of the environment (e.g. state 0 or state 1), the personal information (i.e. perceived cue intensity x) of each decision-maker is independent from that of the others (see §4). Consequently, in a group of size N , the fraction of decision-makers that, based on their personal information, indicate to take action A when the environment is in state 1 is binomially distributed with mean $p_{\text{true}+}$ and variance $p_{\text{true}+}(1 - p_{\text{true}+})/N$. Analogously, when the environment is in state 0, the fraction of decision-makers that indicate to take action A is binomially distributed with mean $p_{\text{false}+}$ and variance $p_{\text{false}+}(1 - p_{\text{false}+})/N$. Thus, with increasing group size N , the fraction of decision-makers that—based on their personal information—indicate to take action A approaches $p_{\text{true}+}$ (or $p_{\text{false}+}$) when the environment is in state 1 (or state 0), because the variance of this fraction approaches zero. Therefore, whenever the probability $p_{\text{true}+}$ of committing true positives exceeds the probability $p_{\text{false}+}$ of false positives, any decision rule that sets the threshold q such that

$$p_{\text{false}+} < q < p_{\text{true}+} \quad (2.1)$$

can effectively deduce the true state of the environment (e.g. predator present or absent; disease present or absent). While perfect discrimination will typically be possible only for very large groups, figure 2c shows that substantial improvements for both true and false positives can be achieved already in relatively small groups of less than 20 individuals.

In sum, our analysis provides two key predictions. First, whenever the true positives $p_{\text{true}+}$ of solitary decision-makers exceed their false positives $p_{\text{false}+}$, a group of decision-makers can—compared with a solitary decision-maker—both increase true positives and decrease false positives simultaneously. Second, this collective intelligence effect is achieved whenever decision-makers use a quorum decision rule that sets its threshold q below the rate of true positives and above the rate of false positives of solitary decision-makers (equation (2.1)).

3. Experiment and results

To test these predictions, we recruited students from the University of Bielefeld, Germany, visitors to an open day of Wageningen University, the Netherlands and visitors to the natural history museum in Berlin, Germany. In total, we tested 436 participants divided over 24 groups (average group size: 18.2; range 9–25) in the following predator-detection test (see the electronic supplementary material).

Each group of individuals entered the test room, and individuals were asked to sit on a chair. For a fixed time period of 2 s, a school of 144 fish (aligned in 9×16 grid) was projected onto a white screen. All fish in this school were identical, except one odd fish, which had either six or seven spines. The other 143 fish had no spines. We instructed our subjects to adopt the following decision rule: ‘If you see no odd fish or an odd fish with 6 spines then it is safe and you should stay. If you see an odd fish with 7 spines then it is dangerous and you should escape’. After 2 s of observing the school, participants had 5 s to take a decision via an electronic keypad (‘polling 1’). We then projected for 5 s a bar chart showing

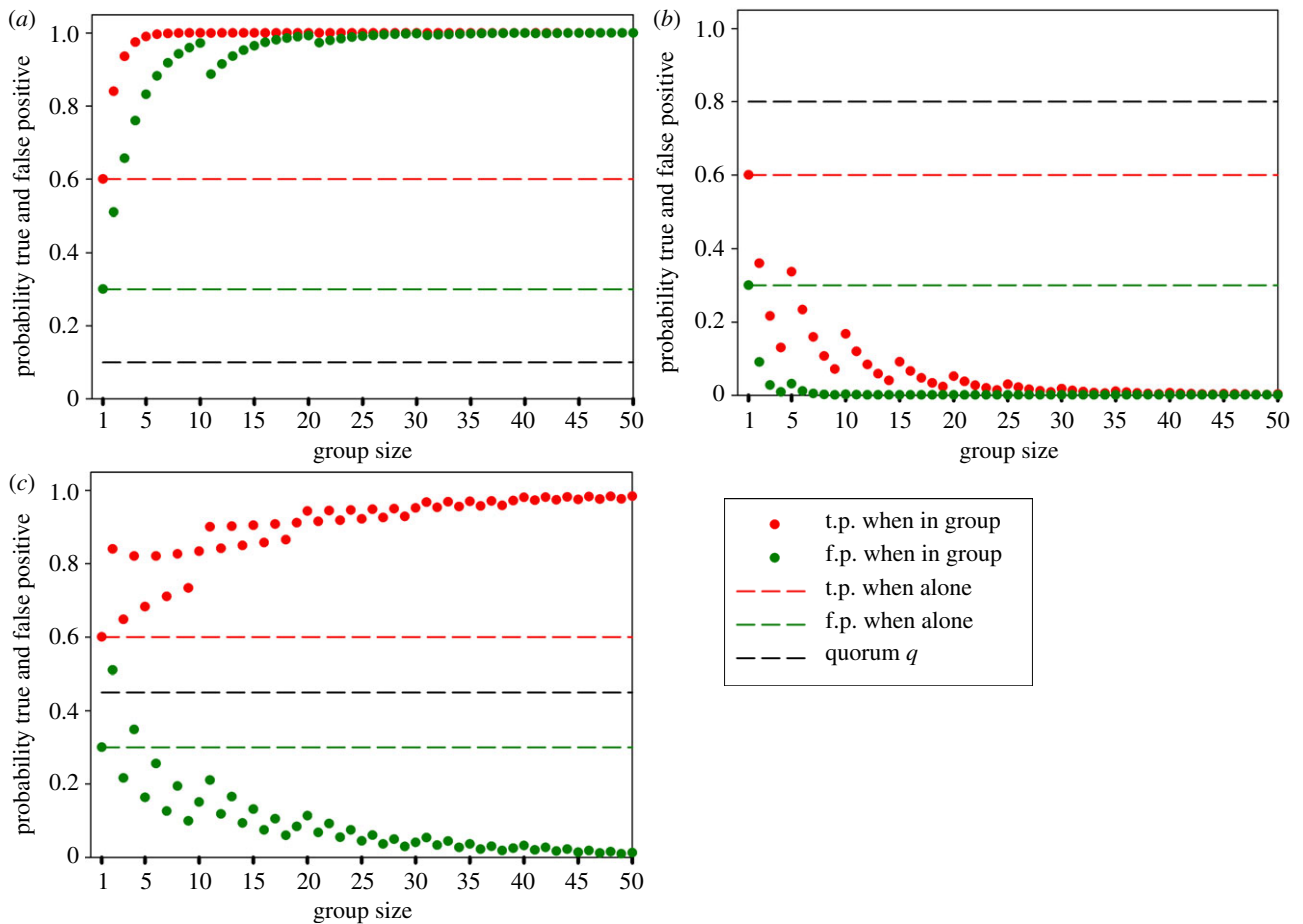


Figure 2. Intermediate quorum thresholds allow decision-makers in groups to overcome the trade-off between true and false positives that solitary decision-makers face. We consider a group of N decision-makers that is confronted with a scenario as depicted in figure 1, each decision-maker uses a decision threshold t that gives rise to true positives $p_{\text{true}+}$ and false positives $p_{\text{false}+}$. We assume that decision-makers use the following 2-step quorum decision rule: ‘indicate to take action A whenever your personal information indicates that you should take action A (i.e. whenever the perceived cue intensity x exceeds the decision threshold t , figure 1), take action A when at least a fraction q of the other group members indicate to take action A ’. The consequences of this rule are illustrated for (a) a low, (b) a high and (c) an intermediate quorum threshold q (hatched black line). (a) For low thresholds ($q = 0.1$), increasing group size gives rise to increased true positives (red dots), but these increases are associated with increased false positives (green dots). (b) For a high thresholds ($q = 0.8$), increasing group size gives rise to decreased false positives, but these decreases are associated with decreased true positives. (c) A very different scenario occurs for intermediate thresholds ($q = 0.45$), where increasing group size is associated with increased true positives and decreased false positives simultaneously. Hence, when using an intermediate threshold (i.e. a threshold below the true positive $p_{\text{true}+}$ and above the false positive $p_{\text{false}+}$, see main text), decision-makers in groups can overcome the trade-off between true and false positives that solitary decision-makers face. All three panels are based on $p_{\text{true}+} = 0.6$, $p_{\text{false}+} = 0.3$ and the assumption that, given the state of the environment (state 0 or state 1), the personal information (perceived cue intensity x) of individuals is independent from that of the others. For each group size, the true and false positives of individuals in groups correspond to the (binomially distributed) probability that, based on their personal information, at least n individuals indicate to take action A in state 0 (true positive) and state 1 (false positive), respectively, where $n = \text{ceil}(q \cdot N)$ is given by the smallest integer that is not less than $q \cdot N$, where q and N correspond to the quorum threshold and group size, respectively.

the number of individuals that decided to escape. Individuals were then asked to decide again (‘polling 2’) after which we presented the results of the second polling and the correct answer (stay or escape). There were two treatments: (i) one fish with six spines and 143 fish without spines, (ii) one fish with seven spines and 143 fish without spines. Each treatment was replicated 14 times resulting in a total of 28 rounds per group. The treatment order and the position of the odd fish were randomized. Prior to the 28 rounds, we performed two test rounds to instruct the participants about the procedure. The results of the test rounds were excluded from our analysis.

We calculated the average true and false positives for each individual before (polling 1) and after (polling 2) observing the decisions of the other group members. Note that a true positive is achieved whenever the seven-spined fish is present and a participant decides to escape; a false positive is committed whenever the six-spined fish

is present and a participant decides to escape. As predicted from our analysis earlier, when comparing the second with the first polling (i.e. after observing the decisions taken by the others), individuals achieved both higher true positives (first polling: mean \pm s.e. = 0.564 ± 0.011 , second polling: 0.751 ± 0.009 , est. \pm s.e. = 0.8604 ± 0.148 , $z = 5.829$, $p < 0.001$) and lower false positives (first polling: mean \pm s.e. = 0.166 ± 0.006 , second polling: 0.113 ± 0.005 ; est. \pm s.e. = -0.448 ± 0.199 , $z = -2.257$, $p = 0.024$). This pattern was very consistent between groups: when comparing polling 2 with polling 1, the average true positive of individuals increased in all of the 24 groups (figure 3a), the average false positive of individuals decreased in 20 of 24 groups (figure 3b). This pattern was also true at the individual level: a large proportion (40.2%) of our 436 participants both increased their true positives and decreased their false positives; and a substantial proportion (28.5%) either

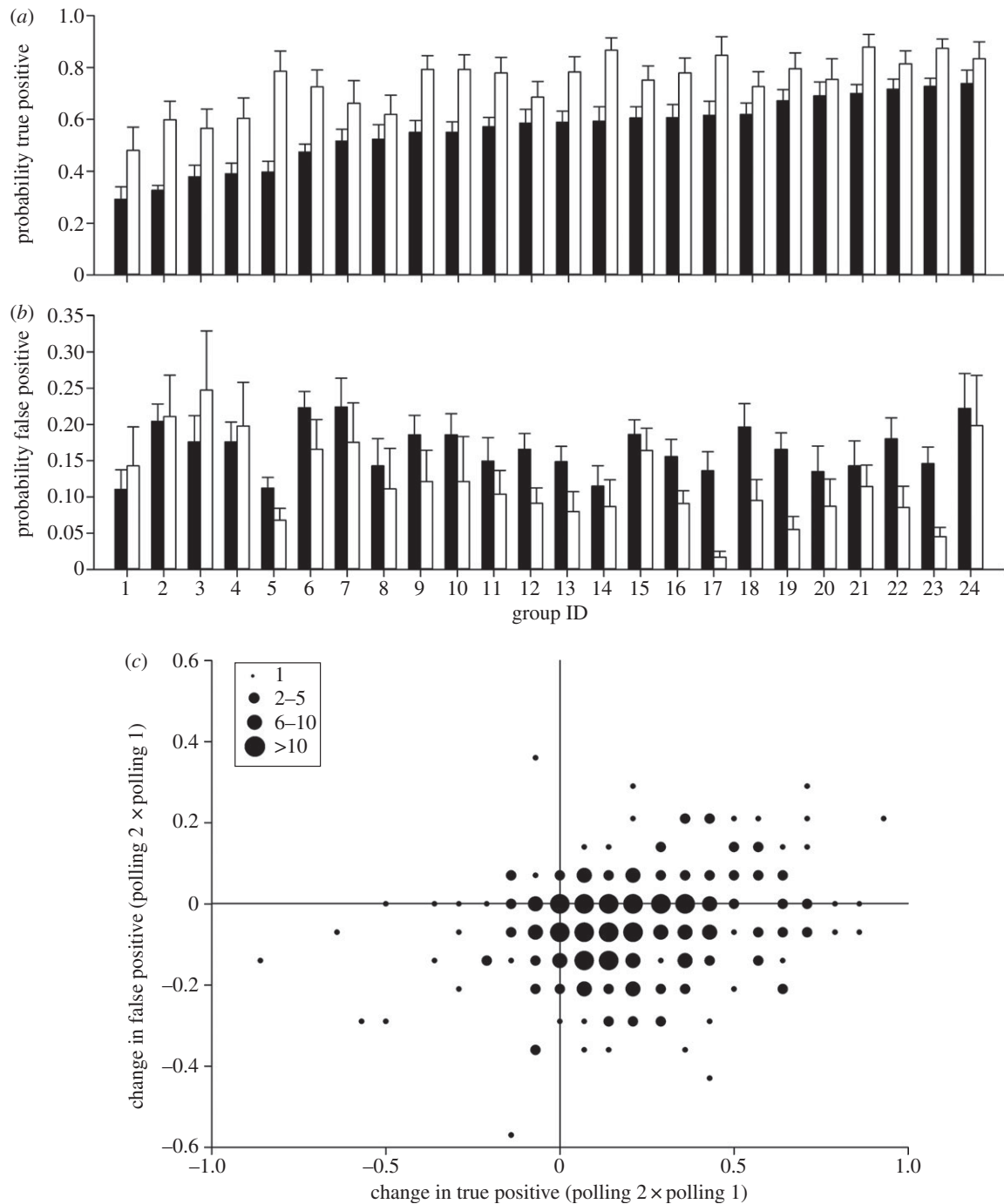


Figure 3. After taking the decision of other group members into account (polling 2), individuals both increase their true positives and decrease their false positives. (a,b) When comparing polling 2 (white bars) with polling 1 (black bars), (a) the average true positive of individuals increased in all 24 groups, (b) the average false positive of individuals decreased in 20 out of 24 groups. Shown are mean \pm s.e.; for clarity, the groups in (a) and (b) are ranked according to their true-positive score of polling 1. (c) This pattern was also true on the individual level: After taking the decision of other group members into account (polling 2), a large proportion (40.2%) of the participants ($N = 436$) both increase true positives and decrease false positives, a substantial proportion (28.5%) either increase true positives with no change in false positives or decrease false positives with no change in true positives. The size of the circles indicates the number of individuals with identical changes in true and false positives.

increased true positives with no change in false positives or decreased false positives with no change in true positives (figure 3c). With increasing group size, there was a larger increase in true positives (est. \pm s.e. = 0.004 ± 0.002 , $t = 2.002$, $p = 0.058$) and a larger decrease in false positives (est. \pm s.e. = 0.003 ± 0.001 , $t = 3.135$, $p = 0.005$).

We investigated whether the participants used quorum responses in their decision to escape in polling 2 based on the social information provided after polling 1. In a quorum response, the probability that an individual decides for a

particular option increases in a step-like way with the number of other individuals that have decided for that option. Such responses can be well described with equation (3.1) [12,13]:

$$p = \frac{x^k}{x^k + T^k}, \quad (3.1)$$

where p is the probability that a focal individual chooses a particular option, x is the number of individuals that have already chosen this option, T is the threshold quorum at

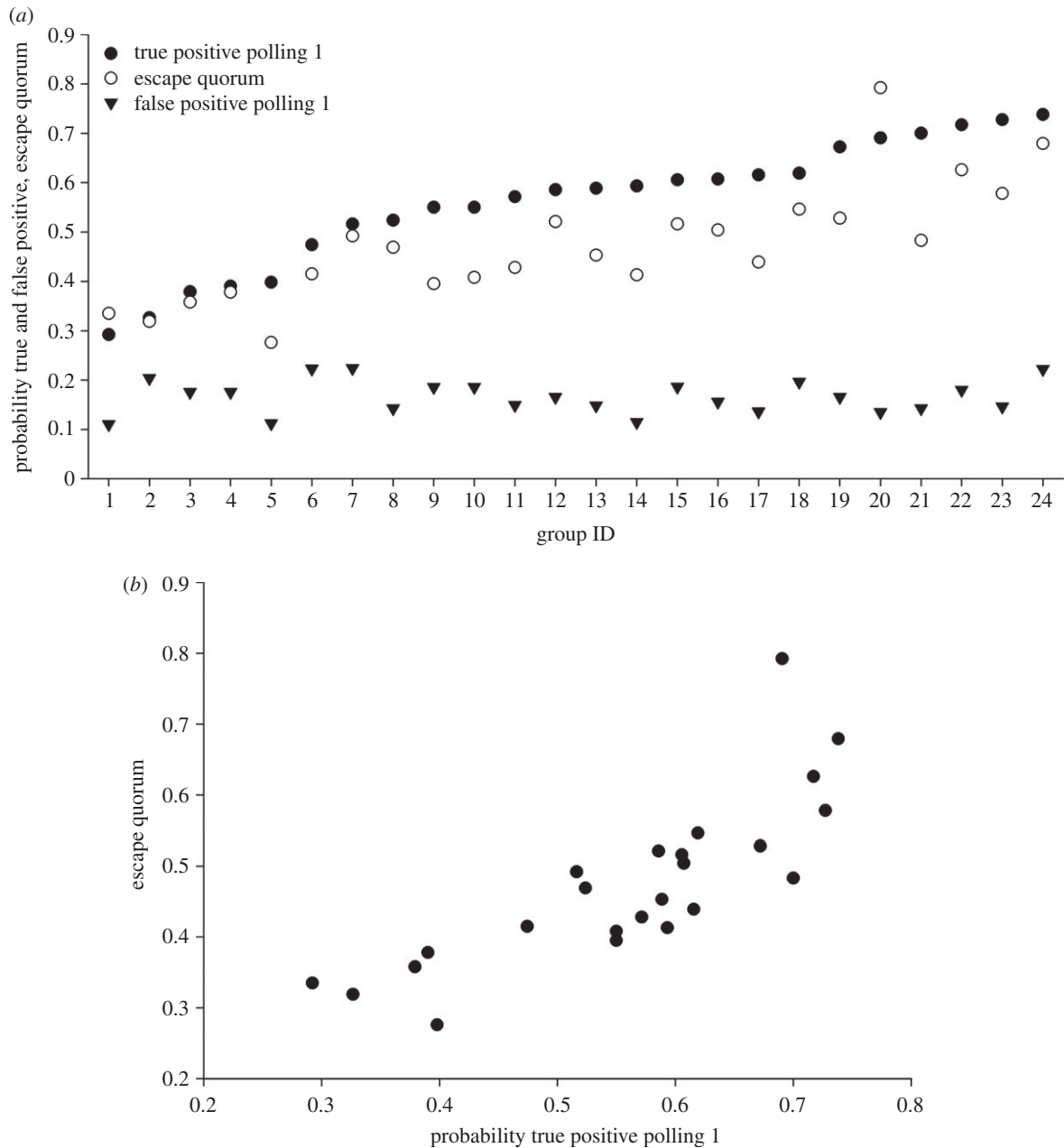


Figure 4. When taking the decisions of the other group members into account, individuals use a quorum threshold set between the average true- and false-positive rates of the other group members. (a) For each group, average true- (filled circle) and false- (filled triangle) positive scores during polling 1 and the estimated escape quorum T (open circle) are shown. The escape quorum corresponds to the quorum threshold at which half of the individuals that decided to stay during polling 1 decided to escape during polling 2 (see the electronic supplementary material). As predicted, for 22 out of 24 of the groups, the escape quorum T lies below the average true-positive score and above the average false-positive score of individuals within that group. (b) There was a strong positive correlation between escape quorum and the average true-positive score during polling 1 (Spearman's $\rho = 0.858$, $p < 0.001$, $n = 24$) suggesting that individuals adaptively adjust their escape quorum in accordance to the performance of the group. For clarity, the groups in (a) are ranked according to the true-positive score of polling 1.

which the response has the steepest increase and k determines the steepness of this increase. As a rule of thumb, a quorum response occurs if $k \geq 2$ [12,13] and higher values of k imply stronger quorum responses. (Note that our mathematical analysis is based on the assumption that individuals use strong quorum responses, that is large k -values. For large k -values, the quorum threshold T corresponds to the quorum threshold q in our mathematical analysis). We estimated the T - and k -values for each group (see the electronic supplementary material). The average k -value was 6.70 (median: 5.14; range: 2.20–28.55), providing strong evidence that individuals used quorum responses.

Figure 4a shows for each group the average true- and false-positive values during polling 1 and the estimated escape quorum T (i.e. the quorum threshold T at which half of the

individuals that decided to stay during polling 1 decided to escape during polling 2; see the electronic supplementary material). In line with our prediction, the escape quorum T —which corresponds to our quorum threshold q above—lies below the average true-positive score and above the average false-positive score of individuals within that group in nearly all groups (22 of 24 groups). Moreover, there was a strong positive correlation between the escape quorum and the average true-positive score during polling 1 (Spearman's $\rho = 0.858$, $p < 0.001$, $n = 24$; figure 4b), indicating that individuals adjusted their escape quorum adaptively to the performance of the group. There was no correlation between the escape quorum and the average false-positive score during polling 1 (Spearman's $\rho = 0.146$, $p = 0.50$, $n = 24$), which can be explained by the small between-group variation in the

average false-positive score in polling 1 (range: 0.11–0.22), as opposed to the large between-group variation in the average true-positive score of polling 1 (range: 0.29–0.74; figure 3*a,b*).

4. Summary and discussion

(a) Summary

Using a mathematical model, we have shown that (i) by joining a group, individuals can both increase true positives and decrease false positives and (ii) this is achieved by a quorum decision rule with a threshold set between true- and false-positive rates of individual decision-makers. The results from a predator-detection test that we performed with humans are consistent with these predictions: (i) after observing the choices of the other group members, individuals both increase true positives and decrease false positives, (ii) this effect gets stronger as group size increases, (iii) individuals use a quorum threshold set between the average true- and false-positive rates of the other group members, and (iv) individuals adjust their quorum adaptively to the performance of the group.

(b) True and false positives of solitary decision-makers

A key assumption in our model is that the true-positive rate of a solitary decision-maker is higher than its false-positive rate. This is a realistic assumption [2]. Our analysis focuses on situations where the environment can be in either of two states, and the decision-maker aims at taking an action *A* in one of the states (state 1: e.g. predator/disease present) but not in the other (state 0: e.g. predator/disease absent). The true positive thus corresponds to the conditional probability $p_{A|state1}$ that the decision-maker takes the action, given that the environment is in state 1; the false positive corresponds to the conditional probability $p_{A|state0}$ that the decision-maker takes the action, given the environment is in state 0. In the extreme case, when the decision-maker has no information about the state of its environment, he/she can only randomize between taking the action or not, independent of the state of its environment, thus giving rise to equal true and false positive, i.e. $p_{A|state1} = p_{A|state0} = p$. Consequently, any information about the true state of the environment will allow the decision-maker to achieve a rate of true positives that is higher than its rate of false positives.

(c) Independence of information

Another key assumption in our model is that, given the state of the environment, the information (i.e. perceived cue intensity *x*, figure 1) held by different decision-makers is independent from each other. Full independence is not required and similar results will be obtained whenever the information of different decision-makers is correlated with each other. Some independence, however, is necessary. Put differently, when all decision-makers always perceive the same cue intensity *x* (figure 1), collective intelligence will not be possible.

In principle, independence of information arises via several potentially interacting mechanisms. First, when decisions have to be made fast (e.g. in an anti-predation context, during a security screen), a single decision-maker may not be able to fully evaluate the situation, and different decision-makers may focus on different aspects of the problem [14–16]. Second, when cues occur only for a brief moment in time and/or in one particular location in space (e.g. cues about a predator in an anti-predation context), the detection of these

cues depends on the position of the decision-maker in space and the direction it faces. Third, when the decision problem is complex and there is no unique best way of evaluating the situation, different decision-makers (e.g. doctors/psychiatrist in a medical/clinical decision-making context) may evaluate identical pieces of information differently, dependent on their experience and cognitive style [17–19].

The fact that collective intelligence as reported here is possible only in the face of some degree of independent information has consequences for our understanding of animal groups and for the improvement of human decision-making processes. Group-living animals may have been shaped by natural selection in order to achieve some degree of independence—e.g. via favouring the synchronization and/or complementation of activities/positioning in space between different group members or via favouring particular mixtures of personality types [20] within a group. Similarly, decision accuracy in contexts such as medical decision-making, job candidate selection, clinical psychology or security screens (table 1) may be improved by group decisions in which decision-makers (i) make decisions without a prior exchange of opinions and (ii) differ in their experience, cognitive style and/or personality [21].

(d) Quorum decision-making

Quorum decision-making can be found in many animal species [13,22–25] ranging from insects to fish to humans. We have shown that quorum decision-making allows individuals in groups to both increase true positives and decrease false positives simultaneously, thereby overcoming a fundamental limitation to decision accuracy that solitary decision-makers face. Our analysis predicts that individuals should adjust their quorum threshold, dependent on the true- and false-positive rates of the other group members. In line with this prediction, we find a strong positive correlation between the escape quorum and the average true-positive score during polling 1 in our experiment (figure 4*b*), indicating that individuals adjust their escape quorum adaptively to the performance of the group. Non-human animals such as ants [26,27] and fish [28] are known to flexibly adjust their response threshold, dependent on environmental conditions. Whether flexible adjustment in response to the decision accuracy of other group members occurs in the way predicted from our model is an interesting open question.

(e) Condorcet's jury theorem

Condorcet's jury theorem [29,30] is a prominent example, illustrating how a group of decision-makers can improve decision accuracy compared with solitary decision-makers. Condorcet's theorem applies to situations where (i) individuals face a binary choice, (ii) each individual has a probability $p > 0.5$ of making a correct decision in the absence of others, and (iii) different decision-makers make their choice independent of each other. Condorcet showed that in such situations, the probability that the majority of individuals make a correct decision increases with group size. While our results may seem to resemble Condorcet's jury theorem, they differ in two key aspects. First, our modelling results are not based on the assumption that individuals have a probability $p > 0.5$ of making a correct decision in the absence of others. Analogously, participants in our experiments often had true positives below 50 per cent (figure 3*a*). Second, our results are not based on majority voting—indeed groups in our experiments often follow a minority of individuals (see the escape quorums in figure 4*b*).

(f) Mechanism of group-decision-making

For simplicity, we investigated situations where decision-makers in groups take a single and final decision after being presented with a summary measure of the decision of all other group members. This is a feasible mechanism in many applied contexts involving human decision-makers (table 1). In many natural situations involving non-human animals, however, both information transfer and decision-making will be more complex [31,32]. Individuals may, for example, not decide simultaneously thus giving rise to a much more dynamic and interdependent ‘voting process’; individuals may repeatedly switch between the different behavioural options; individuals in large groups may observe only the decisions of their local interaction partners. Future studies will investigate how such more complex decision-making mechanisms affect the ability of a group to achieve collective intelligence as reported here.

(g) Individual differences

Our modelling analysis was based on the assumption that all decision-makers are identical. However, in most natural situations—as for example in our experiments—group members may differ in a variety of relevant aspects, including their experience with the particular problem at hand, their cognitive abilities, their general tendency to rely on social information and their propensity to lead a group [33–35]. In our experiments, we have deliberately developed a set-up that minimizes individual differences, in particular, our set-up does not allow for the emergence of leaders and followers. Future studies will investigate how such differences affect the mechanisms of group-decision-making, the individual benefits associated with joining a group (i.e. improvement in decision accuracy) and, ultimately, the ability of a group to achieve collective intelligence as reported here.

(h) Predator avoidance

Research on collective behaviour and group-decision-making in animals has shown that individuals in groups can outperform solitary individuals [31,36–38]. Group-living has important consequences for the performance of individuals in anti-predator contexts [39,40]. Individuals in larger groups have, for example, a lower chance of being killed once detected (dilution and confusion effect) but the chance of being detected by a predator increases with group size. One important dimension of performance under predation risk is decision accuracy when detecting predators. Consequently, a key question is whether individuals in groups can achieve higher decision accuracy than solitary individuals, that is, combinations of true and false positives that are not feasible for solitary individuals.

It is well known that individuals in groups can detect predators earlier and/or with a higher probability than solitary individuals, i.e. achieve higher true positives. The basic intuition underlying this ‘many eyes effect’ [41,42] (also termed

collective detection [4]) is simple: an individual in a group detects the predator not only when it detects the predator itself but also when another group member detects the predator and warns the others (e.g. via an alarm call). Pulliam [43] formalized this idea in an influential model, and several subsequent studies have found this effect empirically [41,44–48]. The same mechanism of social information use, however, is believed to give rise to a decreased performance in the absence of predators (i.e. a higher false positive) [4,7,9,49–51]. In a nutshell, an individual in a group not only commits a false positive when it erroneously detects a predator itself but also when another group member erroneously detects a predator and warns the others. As a consequence, individuals in groups achieve higher true positives than solitary individuals, but this increase comes at a cost of increased false positives, corresponding to the scenario depicted in figure 2*a*.

Our results suggest that groups of animals can do fundamentally better. In particular, when individuals in groups set intermediate response thresholds (i.e. thresholds below the true positive $p_{\text{true}+}$ and above the false positive $p_{\text{false}+}$, see above) they can—compared with solitary individuals—both increase true positives and decrease false positives simultaneously. This result is in line with previous findings that animals in groups can diminish the negative consequences of false positives by using a behavioural rule that does not respond to single but only to multiple other individuals [9,51–54].

(i) General applicability

While our basic arguments and our model apply to a diverse range of decision problems (table 1), in our experiments, we have focused on a predator avoidance context. Future studies will investigate the general applicability of our quorum rule. Multiple doctors may, for example, be presented with a series of cases (e.g. via diagnostic images such as mammography) where the correct diagnosis is known (e.g. cancer present or not). Part of the dataset may be used to estimate true and false positives of individual doctors. These estimates can be used to set a quorum threshold for this group of doctors, which would be used in the remaining part of the dataset. In this set-up, we could evaluate whether our quorum rule allows simultaneous increases in true positives and decreases in false positives in medical diagnostics; similar experiments are conceivable for all other decision contexts mentioned in table 1. As we have stressed repeatedly, our results may be of importance to decision-making in a wide variety of contexts and it will be exciting to further investigate the applicability of our quorum rule in these contexts.

The authors thank four anonymous referees for numerous helpful suggestions on previous versions of the manuscript; the participants of all experiments; Romain Clément and Sander van Doorn for stimulating discussions; Romain Clément, Chantal van Lin, Rudy Jonker, Vincent Comor, Kyle Tomlinson, Leif Engqvist and Julia Roehner for assisting in the experiment. R.H.J.M.K. was funded by an NWO Rubicon grant (no. 825.11.014).

References

1. McNeil BJ, Keeler E, Adelstein SJ. 1975 Primer on certain elements of medical decision making. *New Engl. J. Med.* **293**, 211–215. (doi:10.1056/NEJM197507312930501)
2. Swets JA. 1988 Measuring the accuracy of diagnostic systems. *Science* **240**, 1285–1293. (doi:10.1126/science.3287615)
3. Zweig MH, Campbell G. 1993 Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clin. Chem.* **39**, 561–577.

4. Lima SL. 1995 Collective detection of predatory attack by social foragers: fraught with ambiguity. *Anim. Behav.* **50**, 1097–1108. (doi:10.1016/0003-3472(95)80109-X)
5. Schmidt FL, Hunter JE. 1998 The validity and utility of selection methods in personnel psychology: practical and theoretical implications of 85 years of research findings. *Psychol. Bull.* **124**, 262. (doi:10.1037/0033-2909.124.2.262)
6. Swets JA, Dawes RM, Monahan J. 2000 Psychological science can improve diagnostic decisions. *Psychol. Sci. Publ. Interest* **1**, 1–26. (doi:10.1111/1529-1006.001)
7. Giraldeau LA, Valone TJ, Templeton JJ. 2002 Potential disadvantages of using socially acquired information. *Phil. Trans. R. Soc. Lond. B* **357**, 1559–1566. (doi:10.1098/rstb.2002.1065)
8. Kuncel NR, Hezlett SA. 2007 Assessment: standardized tests predict graduate students' success. *Science* **315**, 1080–1081. (doi:10.1126/science.1136618)
9. Beauchamp G, Ruxton GD. 2007 False alarms and the evolution of antipredator vigilance. *Anim. Behav.* **74**, 1199–1206. (doi:10.1016/j.anbehav.2007.02.014)
10. Green DM, Swets JA. 1966 *Signal detection theory and psychophysics*. New York, NY: Wiley.
11. Macmillan NA, Creelman CD. 2005 *Detection theory: a user's guide*. Mahwah, NJ: Lawrence Erlbaum.
12. Conradt L. 2012 Models in animal collective decision-making: information uncertainty and conflicting preferences. *Interface Focus* **2**, 226–240. (doi:10.1098/rsfs.2011.0090)
13. Sumpter DJT, Pratt SC. 2009 Quorum responses and consensus decision making. *Phil. Trans. R. Soc. B* **364**, 743–753. (doi:10.1098/rstb.2008.0204)
14. Ward AJW, Herbert-Read JE, Sumpter DJT, Krause J. 2011 Fast and accurate decisions through collective vigilance in fish shoals. *Proc. Natl Acad. Sci. USA* **108**, 2312–2315. (doi:10.1073/pnas.1007102108)
15. Chittka L, Skorupski P, Raine NE. 2009 Speed–accuracy tradeoffs in animal decision making. *Trends Ecol. Evol.* **24**, 400–407. (doi:10.1016/j.tree.2009.02.010)
16. Eisenhardt KM. 1989 Making fast strategic decisions in high-velocity environments. *Acad. Manage. J.* **32**, 543–576. (doi:10.2307/256434)
17. Hong L, Page SE. 2004 Groups of diverse problem solvers can outperform groups of high-ability problem solvers. *Proc. Natl Acad. Sci. USA* **101**, 16 385–16 389. (doi:10.1073/pnas.0403723101)
18. Jackson SE, Joshi A, Erhardt NL. 2003 Recent research on team and organizational diversity: SWOT analysis and implications. *J. Manage.* **29**, 801.
19. Liker A, Bokony V. 2009 Larger groups are more successful in innovative problem solving in house sparrows. *Proc. Natl Acad. Sci. USA* **106**, 7893–7898. (doi:10.1073/pnas.0900042106)
20. Wolf M, Weissing FJ. 2012 Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* **27**, 452–461. (doi:10.1016/j.tree.2012.05.001)
21. Lorenz J, Rauhut H, Schweitzer F, Helbing D. 2011 How social influence can undermine the wisdom of crowd effect. *Proc. Natl Acad. Sci. USA* **108**, 9020–9025. (doi:10.1073/pnas.1008636108)
22. Franks NR, Dechaume-Moncharmont FX, Hanmore E, Reynolds JK. 2009 Speed versus accuracy in decision-making ants: expediting politics and policy implementation. *Phil. Trans. R. Soc. B* **364**, 845–852. (doi:10.1098/rstb.2008.0224)
23. Pratt SC, Mallon EB, Sumpter DJ, Franks NR. 2002 Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **52**, 117–127. (doi:10.1007/s00265-002-0487-x)
24. Seeley TD, Visscher PK. 2004 Quorum sensing during nest-site selection by honeybee swarms. *Behav. Ecol. Sociobiol.* **56**, 594–601. (doi:10.1007/s00265-004-0814-5)
25. Ward AJW, Sumpter DJT, Couzin LD, Hart PJB, Krause J. 2008 Quorum decision-making facilitates information transfer in fish shoals. *Proc. Natl Acad. Sci. USA* **105**, 6948–6953. (doi:10.1073/pnas.0710344105)
26. Franks NR, Dornhaus A, Fitzsimmons JP, Stevens M. 2003 Speed versus accuracy in collective decision making. *Proc. R. Soc. Lond. B* **270**, 2457–2463. (doi:10.1098/rspb.2003.2527)
27. Pratt SC, Sumpter DJT. 2006 A tunable algorithm for collective decision-making. *Proc. Natl Acad. Sci. USA* **103**, 15 906–15 910. (doi:10.1073/pnas.0604801103)
28. Ward AJW, Krause J, Sumpter DJT. 2012 Quorum decision-making in foraging fish shoals. *PLoS ONE* **7**, e32411. (doi:10.1371/journal.pone.0032411)
29. Boland PJ. 1989 Majority systems and the Condorcet Jury Theorem. *Statistician* **38**, 181–189. (doi:10.2307/2348873)
30. List C. 2004 Democracy in animal groups: a political science perspective. *Trends Ecol. Evol.* **19**, 168–169. (doi:10.1016/j.tree.2004.02.004)
31. Couzin ID. 2009 Collective cognition in animal groups. *Trends Cognit. Sci.* **13**, 36–43. (doi:10.1016/j.tics.2008.10.002)
32. Deneubourg JL, Goss S. 1989 Collective patterns and decision-making. *Ethol. Ecol. Evol.* **1**, 295–311. (doi:10.1080/08927014.1989.9525500)
33. Kurvers R, Van Oers K, Nolet BA, Jonker RM, Van Wieren SE, Prins HHT, Ydenberg RC. 2010 Personality predicts the use of social information. *Ecol. Lett.* **13**, 829–837. (doi:10.1111/j.1461-0248.2010.01473.x)
34. Dyer JRG, Johansson A, Helbing D, Couzin ID, Krause J. 2009 Leadership, consensus decision making and collective behaviour in humans. *Phil. Trans. R. Soc. B* **364**, 781–789. (doi:10.1098/rstb.2008.0233)
35. Wolf M, McNamara JM. In press. Adaptive between-individual differences in social competence. *Trends Ecol. Evol.*
36. Bonabeau E, Dorigo M, Theraulaz G. 1999 *Swarm intelligence: from natural to artificial systems*. Oxford, UK: Oxford University Press.
37. Camazine S *et al.* 2001 *Self-organization in biological systems*. Princeton, NJ: Princeton University Press.
38. Krause J, Ruxton GD, Krause S. 2010 Swarm intelligence in animals and humans. *Trends Ecol. Evol.* **25**, 28–34. (doi:10.1016/j.tree.2009.06.016)
39. Dehn MM. 1990 Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* **26**, 337–342.
40. Krause J, Ruxton GD. 2002 *Living in groups*. Oxford, UK: Oxford University Press.
41. Powell GVN. 1974 Experimental analysis of social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* **22**, 501–505. (doi:10.1016/S0003-3472(74)80049-7)
42. Lima SL (ed). 1990 *The influence of models on the interpretation of vigilance*, pp. 246–267. Boulder, CO: Westview Press.
43. Pulliam HR. 1973 On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422. (doi:10.1016/0022-5193(73)90184-7)
44. Siegfried WR, Underhill LG. 1975 Flocking as an anti-predator strategy in doves. *Anim. Behav.* **23**, 504–508. (doi:10.1016/0003-3472(75)90126-8)
45. Kenward RE. 1978 Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *J. Anim. Ecol.* **47**, 449–460. (doi:10.2307/3793)
46. Lazarus J. 1979 Early warning function of flocking in birds: experimental study with captive quelea. *Anim. Behav.* **27**, 855–865. (doi:10.1016/0003-3472(79)90023-X)
47. van Schaik C, van Noordwijk M, Warsono B, Sutriano E. 1983 Party size and early detection of predators in sumatran forest primates. *Primates* **24**, 211–221. (doi:10.1007/BF02381083)
48. Cresswell W. 1994 Flocking is an effective anti-predator strategy in redshanks, *Tringa tetanus*. *Anim. Behav.* **47**, 433–442. (doi:10.1006/anbe.1994.1057)
49. Treisman M. 1975 Predation and evolution of gregariousness. II. Economic model for predator–prey interaction. *Anim. Behav.* **23**, 801–825. (doi:10.1016/0003-3472(75)90107-4)
50. Sirot E. 2006 Social information, antipredatory vigilance and flight in bird flocks. *Anim. Behav.* **72**, 373–382. (doi:10.1016/j.anbehav.2005.10.028)
51. Beauchamp G. 2010 Determinants of false alarms in staging flocks of semipalmated sandpipers. *Behav. Ecol.* **21**, 584–587. (doi:10.1093/beheco/arq032)
52. Lima SL. 1994 Collective detection of predatory attack by birds in the absence of alarm signals. *J. Avian Biol.* **25**, 319–326. (doi:10.2307/3677279)
53. Proctor CJ, Broom M, Ruxton GD. 2001 Modelling antipredator vigilance and flight response in group foragers when warning signals are ambiguous. *J. Theor. Biol.* **211**, 409–417. (doi:10.1006/jtbi.2001.2353)
54. Roberts G. 1997 How many birds does it take to put a flock to flight? *Anim. Behav.* **54**, 1517–1522. (doi:10.1006/anbe.1997.0544)