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# Decision accuracy in complex environments is often maximized by small group sizes

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Individuals in groups, whether composed of humans or other animal species, often make important decisions collectively, including avoiding predators, selecting a direction in which to migrate and electing political leaders. Theoretical and empirical work suggests that collective decisions can be more accurate than individual decisions, a phenomenon known as the ‘wisdom of crowds’. In these previous studies, it has been assumed that individuals make independent estimates based on a single environmental cue. In the real world, however, most cues exhibit some spatial and temporal correlation, and consequently, the sensory information that near neighbours detect will also be, to some degree, correlated. Furthermore, it may be rare for an environment to contain only a single informative cue, with multiple cues being the norm. We demonstrate, using two simple models, that taking this natural complexity into account considerably alters the relationship between group size and decision-making accuracy. In only a minority of environments do we observe the typical wisdom of crowds phenomenon (whereby collective accuracy increases monotonically with group size). When the wisdom of crowds is not observed, we find that a finite, and often small, group size maximizes decision accuracy. We reveal that, counterintuitively, it is the noise inherent in these small groups that enhances their accuracy, allowing individuals in such groups to avoid the detrimental effects of correlated information while exploiting the benefits of collective decision-making. Our results demonstrate that the conventional view of the wisdom of crowds may not be informative in complex and realistic environments, and that being in small groups can maximize decision accuracy across many contexts.

## 1. Introduction

Decision-making, such as regarding which food patch to exploit, which individuals to court, or in which direction to migrate, is central to the lives of many organisms and a major determinant of fitness [1–3]. Animals typically make decisions under conditions of uncertainty [4] and must obtain relevant information in order to improve decision accuracy [5]. Environmental cues frequently covary with biologically meaningful features and consequently often serve as a potent source of information [4]: an odour can predict the presence of food, or the rustling of leaves can predict the presence of a predator, etc. A further reduction of uncertainty may be achieved by incorporating social cues into the decision-making process [4,6–15]. It has been suggested that by pooling imperfect estimations, groups may achieve increased decision accuracy, the so-called wisdom of crowds [16–21].

In this view, individual errors in judgement tend to cancel out when imperfect individual estimates are pooled into a consensus choice, leading to a collective decision that is improved with an increasing number of estimates [19]. The earliest theoretical work on this effect dates to 1785 when the Marquis de Condorcet demonstrated that if individuals have a probability  $r > 0.5$  of correctly guessing which of two available options is better, and each guess is statistically independent, then combining a collection of guesses into a

consensus decision through simple majority rule will result in a decision accuracy greater than  $r$  and which increases monotonically with group size, reaching, asymptotically, perfect accuracy for infinitely large groups [20,21].

Recent experiments in simplified laboratory environments have demonstrated that the wisdom of crowds can improve decision accuracy across a variety of contexts, including avoiding a replica predator [22,23] and discriminating between conspecific phenotypes [24], suggesting that this may be an important driver favouring the evolution of sociality. Nonetheless, it is evident in nature that many organisms make decisions alone, and that many social organisms live in relatively small groups [25], seemingly failing to take advantage of the informational benefits of large group size. It has been assumed, previously, that this may be due to constraints that limit group size, such as increased competition for resources [25,26]. However, it is not known whether a balance between the costs and benefits of group-living is the only cause of intermediate group sizes, or if such group sizes can inherently be adaptive, in terms of maximizing individual members' information-processing capability.

Most natural environments in which animal groups live and make decisions are complex [27], especially relative to those typically studied in existing theory and experiments on the wisdom of crowds. Although previous work has considered a single cue (such as a cryptic predator [22–23] and visual differences among individuals [24]), many natural environments are composed of a rich set of cues simultaneously spanning multiple sensory modalities [4,28–30]. These cues, as with other features of natural environments, typically contain some degree of spatial [31,32] and temporal [33] autocorrelation. In general, different cues will tend to have different degrees of observational correlation, and differing reliability in predicting the correct option. In the natural world, these could be cues from different sensory modalities, or cues in a single modality that differ in their degree of correlation (e.g. landmarks may be visible to all individuals within a group and consequently the information provided will be correlated among individuals, whereas other visual cues may be perceived more locally, and will thus provide less correlated information to members of the group). Consequently, the sensory information that many group-living organisms perceive is, to a greater or lesser degree, correlated rather than being statistically independent. Some theory has been developed to explore the consequences of correlated information in voting [34–36] and among sensory neurons [37] and has shown that because diversity of opinion is critical to the wisdom of crowds [17], observational correlation tends to lead to poorer collective decisions. Nonetheless, the robustness of the wisdom of crowds effect in complex environments is still not well understood.

Here, we explore the effect of environmental complexity and information correlation on the ability of animal groups to achieve collective wisdom. We consider collective decision-making in two environments, in order to illustrate two kinds of observational correlation likely to be common in nature, as well as an environment containing both of these general types of correlations. For the sake of simplicity, we study the case of individuals in a group deciding between two discrete options, such as two potential food patches, although the models are amenable to scenarios involving an arbitrary number of options.

Theoretical and empirical work has shown that the social interaction rules adopted by many organisms effectively

integrate the opinions of the group, such that the resulting collective decision often closely mirrors the majority opinion [15,18,22–24,38,39]. Consequently, although they may lack the capacity for numerosity (the ability to explicitly count or tally), or to explicitly cast a 'vote', organisms such as schooling fish do effectively perform majority consensus decision-making through their employment of simple and local social interactions [15,22–24,39]. Furthermore, the presence of individuals lacking preferences has been shown to further promote majority voting by such animal groups [39]. In other organisms, such as in some primates, organisms are thought to use, in addition, signals such as calls or gestures to convey their preference, thus also resulting in a type of voting behaviour [18].

Based on these empirical results, our model of collective decision-making in complex environments is as follows: we assume that in a given decision bout, each group member observes the cue(s) present in the environment and uses a voting strategy to translate these observations into a discrete vote for one of the two available options. These individual votes are then aggregated, and the group makes a consensus decision in favour of the majority preference (simple majority rule). We calculate the probability that a group chooses the correct option, for a given environment, voting strategy and group size. With this model structure, we simplify the collective dynamics for clarity (but without sacrificing realism) while highlighting the effect of the external environment on the wisdom of crowds.

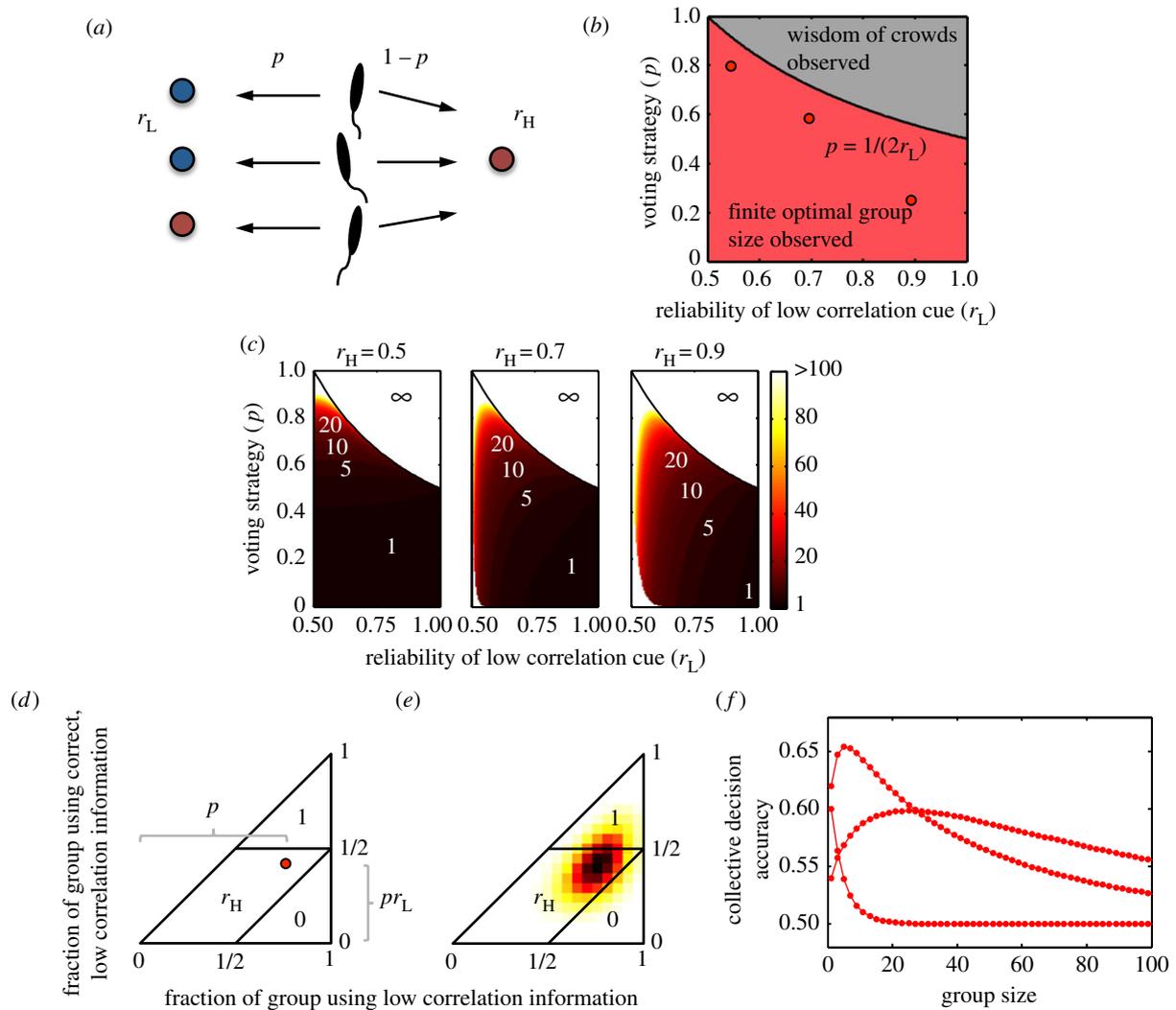
## 2. Results

### (a) Collective decision-making in environments with multiple environmental cues

In the first class of models, we consider multiple cues to be simultaneously present in the environment but that may differ in their degree of observational correlation and reliability. We assume, initially, that individuals make decisions in an environment containing just two cues and later we extend the results to arbitrarily many cues.

In the two-cue model (figure 1*a*), we consider the scenario where one cue has low observational correlation (i.e. independently sampled by individuals) and indicates the correct option with reliability  $r_L$ , whereas the other cue has high observational correlation and has reliability  $r_H$  (figure 1*a*), where the reliability (the probability that it predicts the superior option) can take any value between 0.5 and 1. Each individual's voting strategy is to choose the low correlation cue with probability  $p$  and the high correlation cue with probability  $1 - p$  and to vote for the option indicated by that cue. Majority consensus determines the collective decision [15,18,38,39].

Unlike collective decision-making within simpler environments [21,40], in this complex environment, we observe two regimes of parameter space: for some values of  $r_L$ ,  $r_H$  and  $p$ , we observe what has previously been termed the 'wisdom of crowds' effect (whereby collective accuracy increases monotonically with group size and asymptotes at perfect accuracy for infinitely large groups), whereas for other parameter values, we do not (figure 1*b*). In order for the wisdom of crowds to be guaranteed, the expected proportion of the group receiving correct, low correlation information must exceed  $1/2$ , hence the wisdom of crowds is observed only if  $p > 1/(2r_L)$ . Whether or not animal groups can achieve collective intelligence therefore



**Figure 1.** How an environment containing two cues affects the wisdom of crowds. (a) Diagram of the model scenario showing individuals in a group observing two environmental cues: one cue (left) has low correlation, whereas the other (right) has high correlation. (b) There exist two regimes of parameter space, one in which the wisdom of crowds is observed (grey), and another in which a finite optimal group size is observed (red). (c) The optimal group size across environmental and behavioural space. (d) The space of possible opinion states that a group can be in in a given decision trial, and the accuracy expected in that trial as a function of the group state. In the upper region, the majority of the group uses correct, low correlation information, so the group is guaranteed to make a correct decision. In the left region, the majority is not using correct, low correlation information, but there are sufficiently many individuals using the high correlation cue such that if that cue provided correct information, then there would be a majority using correct information. The group's accuracy is therefore  $r_H$ , because it is contingent on the high correlation cue. In the lower-right region, insufficiently many individuals use correct, low correlation information, and there are insufficiently many individuals using the high correlation cue such that the group will not make a correct decision, even if the high correlation cue is correct. An infinitely large group deterministically finds itself at the point  $(p, pr_L)$ . (e) For finite-sized groups, the probability distribution within opinion space is described by a two-dimensional binomial distribution, which allows for enhanced accuracy if the additional probability of being in the upper region exceeds that of the lower-right region.  $N = 20$ ,  $r_L = 0.55$ ,  $p = 0.75$ . (f) Some examples of how collective accuracy varies with group size in the region where a finite group size is optimal. Values used are shown as points in figure 1b, with  $r_H = 0.5$ .

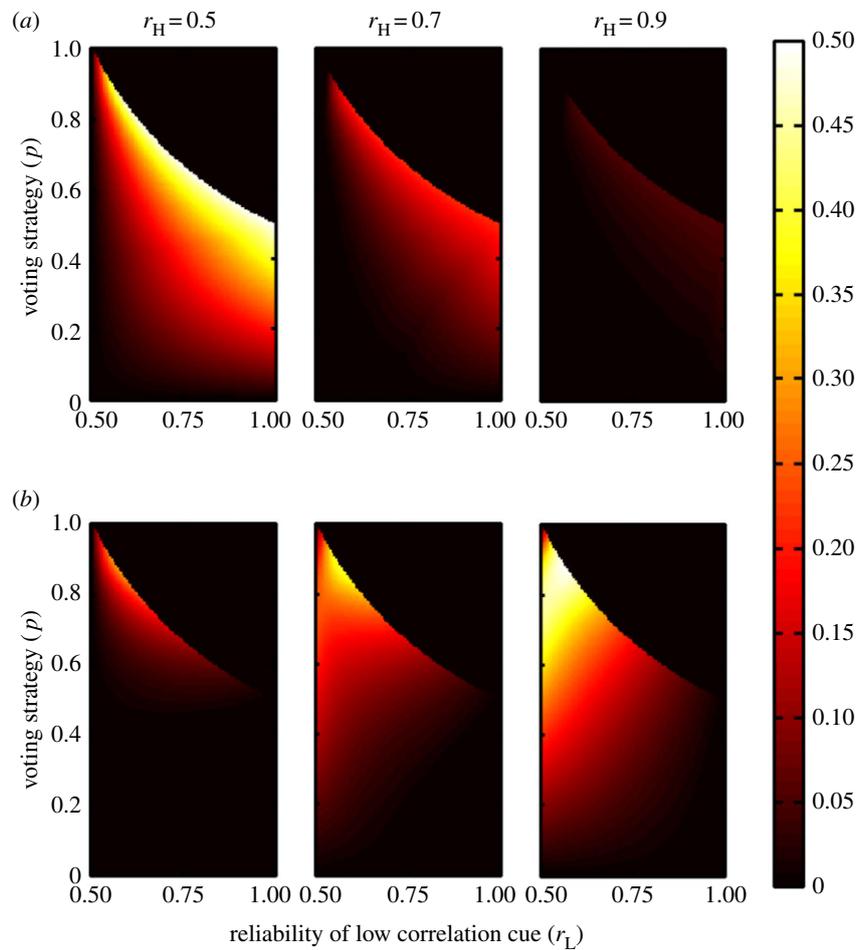
depends on both the animals' behaviour (the voting strategy,  $p$ ) and the properties of the environment (specifically the reliability of the low correlation cue,  $r_L$ ).

If an animal group is in an environment where the wisdom of crowds is not possible ( $p < 1/(2r_L)$ ), then we find that very large groups achieve a collective accuracy of just  $r_H$ . This is because when only a minority of individuals are using correct, low correlation information, there are still sufficiently many individuals using the high correlation cue such that if that cue provides correct information, then a majority of the group will still vote correctly. Under these conditions, the group reaches the correct decision only if the high correlation cue is correct. Consequently, in this regime, the group decision is essentially dictated by the high correlation cue, and this cue

can control the group decision even when only a minority of the group uses the cue, i.e. when  $1/2 < p < 1/(2r_L)$ . This highlights the strong potential of highly correlated information to undermine the wisdom of crowds.

### (b) The role of noise and effective consensus decision-making

In environments where the wisdom of crowds is not possible ( $p < 1/(2r_L)$ ), we find that there exists an optimal, finite group size that maximizes decision accuracy, and that this group size tends to be moderately small, but greater than 1 (figure 1c). To understand why this is the case we investigate the role of noise (stochastic error) during collective decision-making.



**Figure 2.** Accuracy of optimally sized groups. Increase in accuracy (a) relative to infinitely large groups and (b) relative to solitary individuals, across voting strategies and environments where a finite group size is optimal. When  $r_H$  is low (left column), there is a substantial increase in collective accuracy compared with infinitely large groups, but only a minor improvement over solitary individuals. When  $r_H$  is high (right column), the converse is true.

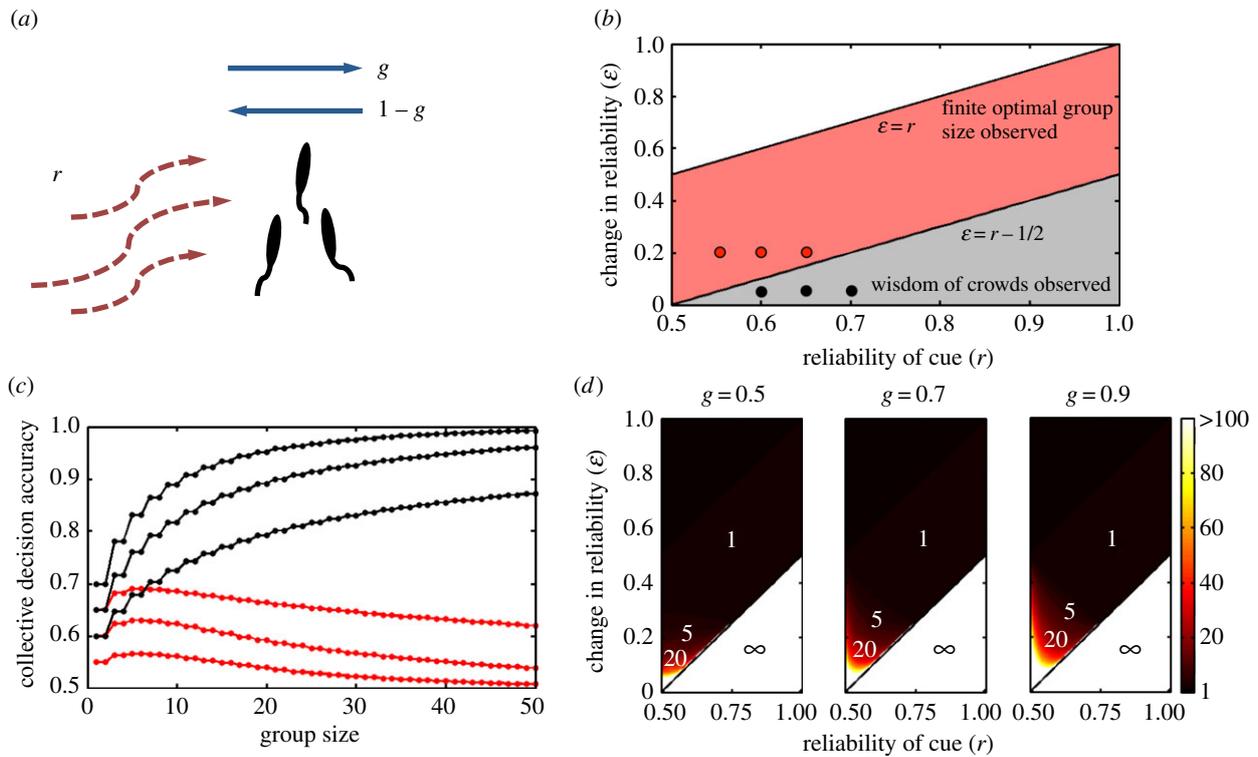
Finite-sized groups are subjected to binomial noise along two dimensions: one relating to how many individuals use each cue (a function of the voting strategy  $p$ ), and the other relating to how many individuals, out of those who use the low correlation cue, receive correct information (a function of the reliability  $r_L$ ). We can succinctly describe the distribution of opinions in the group with these two parameters (figure 1*d,e*). Although very large groups are deterministically placed at a single point in this space (figure 1*d*), finite-size groups exhibit a probability distribution in opinion space (figure 1*e*).

The consequence of such noise on collective accuracy is dependent on the environment. When the wisdom of crowds is possible ( $p > 1/(2r_L)$ ), the noise is always detrimental to collective accuracy because it increases the probability that a group experiences lower accuracy regions of opinion space, when compared with infinitely large groups. By contrast, when the wisdom of crowds is not possible ( $p < 1/(2r_L)$ ), noise can have the converse effect, allowing the collective accuracy of some group sizes to exceed that of infinitely large groups (figure 1*f*). Because noise increases asymmetrically with changes in group size (with respect to the geometry of the space of opinion states), these group sizes are able to increase their probability of experiencing high accuracy regions of opinion space faster than the rate of increase of the probability of experiencing low accuracy regions (figure 1*e*), thereby allowing individuals in such groups to exceed the accuracy of those in larger, or infinitely large, groups.

In this regime, the improvement in decision accuracy at the optimal group size, when compared with infinitely large groups (figure 2*a*) and to solitary individuals (figure 2*b*), depends largely on the reliability  $r_H$  of the high correlation cue. When  $r_H$  is small ( $\approx 0.5$ ), the optimal group size shows a large improvement over infinitely large groups and only a small improvement over solitary individuals. When  $r_H$  is large ( $\approx 1$ ), the reverse is true. The presence of noise in small groups may therefore substantially improve individuals' ability to make decisions collectively (regarding, for example, finding food or avoid predators) when compared with other group sizes.

### (c) Fraction of environments that allow for the wisdom of crowds

In our analysis so far, we have assumed that an animal's voting strategy  $p$  can be an arbitrary value between 0 and 1 in any environment. However, it is well known that animals typically learn and tune their behaviour in response to the properties of environmental cues [41,42]. Because there is no evidence that animals can detect the observational correlation of a cue among individuals (although to our knowledge, there have been no direct tests of this), we may expect  $p$  to be a function only of the reliability of the cues. There are three strategies that animals may reasonably exhibit: they exclusively use the more reliable cue (maximizing strategy) [43], they use a cue proportionally to its reliability (matching strategy) [43], or



**Figure 3.** How an environment containing a fluctuating cue affects the wisdom of crowds. (a) Diagram of model scenario. There is one cue, which individuals independently sample, and which has reliability  $r$ . With probability  $g$ , all individuals have an increased probability  $r + \varepsilon$  of receiving correct information from the cue, and with probability  $1 - g$  have a decreased probability  $r - \varepsilon$  of receiving correct information. Individual opinions are then aggregated into a consensus decision through simple majority rule, as in the previous model. (b) The wisdom of crowds is observed only if  $\varepsilon < r - 1/2$ ; otherwise, an infinitely large group will achieve an accuracy of  $g$ . (c) The emergence of the wisdom of crowds depends on the environment, as in the previous model. Parameter values used are shown as points in figure 3b, with  $g = 0.5$ . (d) The optimal group size across environmental space. Compared with the previous model, the space in which moderate group sizes are optimal is small. Instead, for most of parameter space, the optimal group size is either infinitely large, or one.

they choose each cue with equal probability (random strategy). We calculate the fraction of parameter space (values of  $r_L$  and  $r_H$ ) in which the wisdom of crowds would be observed using each of these strategies, and find the proportion to be 50% for the maximizing strategy, 18% for the matching strategy, whereas the wisdom of crowds is never observed for the random strategy, compared with 31% of scenarios when the environment and behaviour are not coupled (see electronic supplementary material for details). Therefore, even when individuals are capable of tuning their behaviour to the environmental contingencies, they are still highly limited in their ability to achieve the wisdom of crowds.

#### (d) Environments with arbitrarily many environmental cues

We extend our analysis to include arbitrarily many environmental cues. We suppose  $M$  cues,  $M_L$  of which have low observational correlation, and  $M - M_L$  of which have high observational correlation, and all cues have arbitrary reliabilities between 0.5 and 1. We again consider the three possible voting strategies previously described, plus the strategy where individuals favour the option that the majority of the observed cues indicate is correct (the majority strategy). Here, we find that the emergence of the wisdom of crowds relates closely to the fraction of the cues that have low correlation ( $M_L/M$ ) and is again dependent on voting strategy used. For the maximizing strategy, the probability is equal to  $M_L/M$ ; for the matching strategy, it occurs only if  $M_L/M > \langle r \rangle_M / (2\langle r^2 \rangle_L)$ ; and for both the random and majority strategies, it occurs only if  $M_L/M >$

$1/(2\langle r \rangle_L)$ , where  $\langle \rangle_L$  is the mean across the low correlation cues, and  $\langle \rangle_M$  is the mean across all of the cues (see electronic supplementary material for details).

#### (e) Modelling correlated fluctuations in cue reliability

To investigate further the importance of observational correlations in collective decision-making, we develop a second model, in which we reduce the environment to one cue, which for concreteness we imagine to be a dissolved odour in water that indicates which of two patches contains food (figure 3a). Here, the cue is independently sampled by the group members, and each member has a probability  $r$  of receiving correct information from the cue. However, water is subjected to currents and turbulence, which can globally affect group members' probability of receiving correct information from the cue [44–46]. We consider that with a probability  $g$ , the water current is such that the probability that each individual receives correct information increases to  $r + \varepsilon$ , whereas with probability  $1 - g$ , the probability decreases to  $r - \varepsilon$  (figure 3a). Individuals favour the option that their observation of the cue indicates, and a consensus decision is formed through simple majority rule, as before.

We find that similar to the first model, the capacity for individuals to benefit from the wisdom of crowds is dependent on the environment (figure 3b,c). Here, the condition for this phenomenon to emerge is  $\varepsilon < r - 1/2$ , which only occurs in one-third of possible environments (figure 3b). In all other environments, an infinitely large group attains an

accuracy of only  $g$ . Smaller groups again outperform larger groups, and for similar reasoning as previously discussed: as group size shrinks, noise increases asymmetrically, such that the collective decision accuracy increases. In contrast to the first model, however, the region in which moderately sized groups are optimal is small, and generally either single (solitary) individuals or infinitely large groups are optimal (figure 3*d*).

### (f) Combining the two forms of correlation

The two kinds of correlation described above could coexist simultaneously in a natural environment. Multiple cues may abound, with different reliabilities and correlations, and these reliabilities may be subjected to occasional, large-scale disturbances owing to currents, turbulence or gusts. In a simple model containing both kinds of correlations, we imagine two cues, one with low correlation and one with high correlation. With probability  $g$ , the reliability of the low correlation cue is  $r_L + \varepsilon$ , and with probability  $1 - g$ , the reliability is  $r_L - \varepsilon$ . The reliability of the high correlation cue is  $r_H$ . In this scenario, the wisdom of crowds is guaranteed only if  $p > 1/(2(r_L - \varepsilon))$ . The proportion of environments that satisfies this requirement is found by integrating the geometric regions shown in figure 1*b* and figure 3*b* and is given by  $8/3 \int_{1/2}^1 \int_0^{r_L-1/2} (1 - 1/2(r_L - \varepsilon)) d\varepsilon dr = 0.076$ .

## 3. Conclusion

We have demonstrated that explicitly taking into account environmental complexity, such as multiple cues, and the presence of observational correlation in the cues, substantially alters our view of how collective intelligence is achieved by groups. Under such conditions, which are likely to be the norm, not the exception, in most natural environments [4,27], we find that small, or intermediate-sized, groups typically outperform those that are large. It is shown that it is the noise inherent in small groups that results in their enhanced performance by allowing individuals in small groups to ‘escape’ the constraints of highly correlated information while retaining some of the benefits of pooling information collectively.

Our results suggest that small or intermediate group sizes, as are commonly observed in nature [25–26], may maximize the informational benefits of sociality when individuals make decisions collectively. Consequently, it may not be necessary to invoke a trade-off between the benefits and costs of sociality to explain why some animals maintain small group size. We propose that group-living organisms may take advantage of the noise inherent in small groups, enhancing decision accuracy in the particular environment in which they live.

Conversely, the decisions of very large groups may be highly accurate when the information used is independently sampled, but they are particularly susceptible to the negative effects of correlated information, even when only a minority of the group uses such information. Some group-living organisms do form very large groups, including some species of flocking birds, swarming insects and herding ungulates. Despite such groups appearing similar in structure and form, there can often be greatly differing selection pressures that underlie the formation of groups. For example, vast mobile swarms of locusts are on a ‘forced march’ driven by limiting essential nutrients [47] and cannibalistic interactions [47–49].

Aggregations are particularly common during seasonal migration [50] for breeding purposes [51] and environmental factors, such as limiting food or water availability [52] or high predation risk [53], may all contribute to the formation of groups.

While individuals can benefit from being in large groups for certain problem-solving tasks (e.g. large groups can span and sense long-range environmental gradients undetectable by individuals [54]), group size may not always be the relevant quantity when considering information processing and decision-making. In some groups, despite their size, only relatively few individuals contribute to decision-making. For example, in hierarchical societies, a small fraction of the group, based on dominance, age or experience, may decide where and when to travel [55–57]. Furthermore, evolutionary models suggest that if personal information, on which decisions must be made, is costly to acquire, then groups may consist of a small subset of individuals that acquires environmental cues (producers) [58,59] and a larger subset of ‘followers’ (scroungers) [60]. Nonetheless, collective decision-making is not impeded by the presence of uninformed individuals in the group; information can be effectively transmitted without requiring signalling or individual recognition [38–39], and uninformed individuals may even speed up and increase the sensitivity of decision-making [61]. Therefore, even when groups are large, the number of individuals contributing to a group’s decision may be relatively small, which may allow some large groups to retain the accurate decision-making capabilities we reveal here.

Correlation in opinions may be an understudied, but critical, aspect of collective decision-making. It alters the landscape of decision accuracy, such that collective wisdom is maximized by small groups in most environments. Our results suggest that small groups may constitute an effective strategy, whereby collective wisdom is still harnessed but remains robust to highly correlated information. Collective intelligence also has wide applicability in human decision-making, including law-making bodies, prediction markets and corporations. While there is growing evidence that the wisdom of crowds leads to substantially improved decision accuracy [16–20,62], it is still not well understood how it operates in complex, real-world conditions. For example, how social information is shared between group members can affect the resulting decision accuracy [40] and can often undermine the wisdom of crowds by improving confidence in the collective decision without improving its accuracy [63]. Here, we have shown that the external environment from which group members draw information can also substantially affect the wisdom of crowds by introducing correlations in group members’ opinions. Humans often gather information from common, and correlated, sources such as news networks and influential individuals, and world events can have global effects on people’s opinions. Quantifying these correlations and understanding their effect on collective intelligence is likely to be crucial to understand the evolution of sociality and to exploit effectively collective intelligence to improve decisions in human endeavours.

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## References

- Sih A. 1980 Optimal behavior: can foragers balance two conflicting demands? *Science* **210**, 1041–1043. (doi:10.1126/science.210.4473.1041)
- Ydenberg RC, Dill LM. 1986 The economics of fleeing from predators. *Adv. Stud. Behav.* **16**, 229–249.
- Dill LM. 1986 Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Can. J. Zool.* **65**, 803–811. (doi:10.1139/z87-128)
- Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193. (doi:10.1016/j.tree.2005.01.010)
- Hein AM, McKinley SA. 2012 Sensing and decision-making in random search. *Proc. Natl Acad. Sci. USA* **109**, 12 070–12 074. (doi:10.1073/pnas.1202686109)
- Danchin E, Giraldeau L-A, Valone TJ, Wagner RH. 2004 Public information: from nosy neighbors to cultural evolution. *Science* **305**, 487–491. (doi:10.1126/science.1098254)
- Pike TW, Kendal JR, Rendell LE, Laland KN. 2010 Learning by proportional observation in a species of fish. *Behav. Ecol.* **21**, 570–575. (doi:10.1093/beheco/arq025)
- Kendal RL, Coolen I, van Bergen Y, Laland KN. 2005 Trade-offs in the adaptive use of social and asocial learning. *Adv. Stud. Behav.* **35**, 333–379.
- van Bergen Y, Coolen I, Laland KN. 2004 Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proc. R. Soc. Lond. B* **271**, 957–962. (doi:10.1098/rspb.2004.2684)
- Pike TW, Laland KN. 2010 Conformist learning in nine-spined sticklebacks' foraging decisions. *Biol. Lett.* **6**, 466–468. (doi:10.1098/rsbl.2009.1014)
- Coolen I, Ward AJW, Hart PJB, Laland KN. 2005 Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. *Behav. Ecol.* **16**, 865–870. (doi:10.1093/beheco/ari064)
- Webster MM, Laland KN. 2008 Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proc. R. Soc. B* **275**, 2869–2876. (doi:10.1098/rspb.2008.0817)
- Webster MM, Laland KN. 2012 The learning mechanism underlying public information use in ninespine sticklebacks (*Pungitius pungitius*). *J. Comp. Psychol.* **127**, 154–165. (doi:10.1037/a0029602)
- Morgan TJH, Rendell LE, Ehn M, Hoppitt W, Laland KN. 2012 The evolutionary basis of human social learning. *Proc. R. Soc. B* **279**, 653–662. (doi:10.1098/rspb.2011.1172)
- Arganda S, Pérez-Escudero A, de Polavieja GG. 2012 A common rule for decision making in animal collectives across species. *Proc. Natl Acad. Sci. USA* **109**, 20 508–20 513. (doi:10.1073/pnas.1210664109)
- Galton F. 1907 Vox populi. *Nature* **75**, 450–451. (doi:10.1038/075450a0)
- Surowiecki J. 2004 *The wisdom of the crowds: why the many are smarter than the few*. London, UK: Little Brown.
- Conradt L, List C. 2009 Group decisions in humans and animals: a survey. *Phil. Trans. R. Soc. B* **364**, 719–742. (doi:10.1098/rstb.2008.0276)
- Simons AM. 2004 Many wrongs: the advantage of group navigation. *Trends Ecol. Evol.* **19**, 453–455. (doi:10.1016/j.tree.2004.07.001)
- Condorcet M. 1785 *Essai sur l'application de l'analyse à la probabilité des décisions rendues à la pluralité des voix*. Paris, France: Imprimerie Royale.
- King AJ, Cowlishaw G. 2007 When to use social information: the advantage of large group size in individual decision making. *Biol. Lett.* **3**, 137–139. (doi:10.1098/rsbl.2007.0017)
- Ward AJW, Herbert-Read JE, Sumpter DJT, Krause J. 2011 Fast and accurate decision through collective vigilance in fish shoals. *Proc. Natl Acad. Sci. USA* **108**, 2312–2315. (doi:10.1073/pnas.1007102108)
- Ward AJW, Sumpter DJT, Couzin ID, 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)
- Sumpter DJT, Krause J, James R, Couzin ID, Ward AJW. 2008 Consensus decision making by fish. *Curr. Biol.* **18**, 1773–1777. (doi:10.1016/j.cub.2008.09.064)
- Sumpter DJT. 2010 *Collective animal behavior*. Princeton, NJ: Princeton University Press.
- Krause J, Ruxton GD. 2002 *Living in groups*. Oxford, UK: Oxford University Press.
- McNamara JM, Houston AI. 2009 Integrating function and mechanism. *Trends Ecol. Evol.* **24**, 670–675. (doi:10.1016/j.tree.2009.05.011)
- Painter KJ, Maini PK, Othmer HG. 2000 Development and applications of a model for cellular response to multiple chemotactic cues. *J. Math. Biol.* **41**, 285–314. (doi:10.1007/s002850000035)
- Heit B, Tavener S, Raharjo E, Kubers P. 2002 An intracellular signaling hierarchy determines direction of migration in opposing chemotactic gradients. *J. Cell Biol.* **159**, 91–102. (doi:10.1083/jcb.200202114)
- Candolin U. 2003 The use of multiple cues in mate choice. *Biol. Rev.* **78**, 575–595. (doi:10.1017/S1464793103006158)
- Ruderman DL, Bialek W. 1994 Statistics of natural images: scaling in the woods. *Phys. Rev. Lett.* **73**, 814–817. (doi:10.1103/PhysRevLett.73.814)
- Legendre P, Fortin M-J. 1989 Spatial pattern and ecological analysis. *Vegetatio* **80**, 107–138. (doi:10.1007/BF00048036)
- Simoncelli EP, Olshausen BA. 2001 Natural image statistics and neural representations. *Annu. Rev. Neurosci.* **24**, 1193–1216. (doi:10.1146/annurev.neuro.24.1.1193)
- Ladha KK. 1992 The Condorcet jury theorem, free speech, and correlated votes. *Am. J. Polit. Sci.* **36**, 617–634. (doi:10.2307/2111584)
- Shapley L, Grofman B. 1984 Optimizing group judgmental accuracy in the presence of interdependencies. *Public Choice* **43**, 329–343. (doi:10.1007/BF00118940)
- Kaniovski S. 2010 Aggregation of correlated votes and Condorcet's jury theorem. *Theory Dec.* **69**, 453–468. (doi:10.1007/s11238-008-9120-4)
- Zohary E, Shadlen MN, Newsome WT. 1994 Correlated neuronal discharge rate and its implications for psychophysical performance. *Nature* **370**, 140–143. (doi:10.1038/370140a0)
- Couzin ID, Krause J, Franks NR, Levin SA. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)
- Couzin ID, Ioannou CC, Demirel G, Gross T, Torney CJ, Hartnett A, Conradt L, Levin SA, Leonard NE. 2011 Uninformed individuals promote democratic consensus in animal groups. *Science* **334**, 1578–1580. (doi:10.1126/science.1210280)
- King AJ, Cheng L, Starke SD, Myatt JP. 2012 Is the true 'wisdom of the crowd' to copy successful individuals? *Biol. Lett.* **8**, 197–200. (doi:10.1098/rsbl.2011.0795)
- Miller R, Escobar M. 2002 Learning: laws and models of basic conditioning. In *Stevens' handbook of experimental psychology*, vol. 3: *learning, motivation, and emotion* (eds H Pashler, R Gallistel), pp. 47–102. New York, NY: Wiley.
- Gallistel CR. 1990 *The organization of learning*. Cambridge, MA: MIT Press.
- Herrnstein RJ, Loveland DH. 1975 Maximizing and matching on concurrent ratio schedules. *J. Exp. Anal. Behav.* **24**, 107–116. (doi:10.1901/jeab.1975.24-107)
- Vergassola M, Villermaux E, Shraiman BI. 2007 'Infotaxis' as a strategy for searching without gradients. *Nature* **445**, 406–409. (doi:10.1038/nature05464)
- Shraiman BI, Siggla ED. 2000 Scalar turbulence. *Nature* **405**, 639–646. (doi:10.1038/35015000)

46. Sigg H, Stolba A. 1981 Home range and daily march in Hamadryas baboons. *Folia Primatol.* **36**, 40–75. (doi:10.1159/000156008)
47. Bazazi S, Romanczuk P, Thomas S, Schimansky-Geier L, Hale JJ, Miller GA, Sword GA, Simpson SJ, Couzin ID. 2011 Nutritional state and collective motion: from individuals to mass migration. *Proc. R. Soc. B* **278**, 356–363. (doi:10.1098/rspb.2010.1447)
48. Bazazi S, Buhl J, Hale JJ, Anstey ML, Sword GA, Simpson SJ, Couzin ID. 2008 Collective motion and cannibalism in locust migratory bands. *Curr. Biol.* **18**, 735–739. (doi:10.1016/j.cub.2008.04.035)
49. Guttal V, Romanczuk P, Simpson SJ, Sword GA, Couzin ID. 2012 Cannibalism as a driver of the evolution of behavioral phase polyphenism in locusts. *Ecol. Lett.* **15**, 1158–1166. (doi:10.1111/j.1461-0248.2012.01840.x)
50. Baker RR. 1978 *The evolutionary ecology of animal migration*. New York, NY: Holmes and Meier.
51. Makris NC, Ratilal P, Jagannathan S, Gong Z, Andrews M, Bertsatos I, Godo OR, Nero RW, Jech JM. 2009 Critical population density triggers rapid formation of vast oceanic fish shoals. *Science* **323**, 1734–1737. (doi:10.1126/science.1169441)
52. Collett M, Despland E, Simpson SJ, Krakauer DC. 1998 Spatial scales of desert locust gregarization. *Proc. Natl Acad. Sci. USA* **95**, 13 052–13 055. (doi:10.1073/pnas.95.22.13052)
53. Ioannou CC, Guttal V, Couzin ID. 2012 Predatory fish select for coordinated collective motion in virtual prey. *Science* **337**, 1212–1215. (doi:10.1126/science.1218919)
54. Berdahl A, Torney CJ, Ioannou CC, Faria JJ, Couzin ID. 2013 Emergent sensing of complex environments by mobile animal groups. *Science* **339**, 574–576. (doi:10.1126/science.1225883)
55. King AJ, Douglas CMS, Huchard E, Isaac NJB, Cowlshaw G. 2008 Dominance and affiliation mediate despotism in a social primate. *Curr. Biol.* **18**, 1833–1838. (doi:10.1016/j.cub.2008.10.048)
56. Nagy M, Ákos Z, Biro D, Vicsek T. 2010 Hierarchical group dynamics in pigeon flocks. *Nature* **464**, 890–893. (doi:10.1038/nature08891)
57. Mueller T, O'Hara RB, Converse SJ, Urbaneck RP, Fagan WF. 2013 Social learning of migratory performance. *Science* **341**, 999–1002. (doi:10.1126/science.1237139)
58. Guttal V, Couzin ID. 2010 Social interactions, information use and the evolution of collective migration. *Proc. Natl Acad. Sci. USA* **107**, 16172–16177. (doi:10.1073/pnas.1006874107)
59. Torney C, Levin SA, Couzin ID. 2010 Specialization and evolutionary branching within migratory populations. *Proc. Natl Acad. Sci. USA* **107**, 20 394–20 399. (doi:10.1073/pnas.1014316107)
60. Giraldeau LA, Caraco T. 2000 *Social foraging theory*. Princeton, NJ: Princeton University Press.
61. Leonard NE, Shen T, Nabet B, Scardovi L, Couzin ID, Levin SA. 2012 Decision versus compromise for animal groups in motion. *Proc. Natl Acad. Sci. USA* **109**, 227–232. (doi:10.1073/pnas.1118318108)
62. Arrow KJ *et al.* 2008 The promise of prediction markets. *Science* **320**, 877–878. (doi:10.1126/science.1157679)
63. 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)