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Opinion Individual Confidence-Weighting and Group Decision-Making

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Group-living species frequently pool individual information so as to reach consensus decisions such as when and where to move, or whether a predator is present. Such opinion-pooling has been demonstrated empirically, and theoretical models have been proposed to explain why group decisions are more reliable than individual decisions. Behavioural ecology theory frequently assumes that all individuals have equal decision-making abilities, but decision theory relaxes this assumption and has been tested in human groups. We summarise relevant theory and argue for its applicability to collective animal decisions. We consider selective pressure on confidence-weighting in groups of related and unrelated individuals. We also consider which species and behaviours may provide evidence of confidence-weighting, paying particular attention to the sophisticated vocal communication of cooperative breeders.

The Wisdom of the Crowd

It has long been noted that the decisions or estimates of groups can be much more accurate than those of individuals [1], a fact that has gained renewed interest in recent years [2]. Biologists have also been inspired by the power of groups, motivating this through the rediscovery of the Condorcet jury theorem or **Condorcet vote** (see Glossary) [3,4], a result from 19th Century decision theory that explains how collective decisions are more accurate than individual ones [5], supported by experimental tests, for example in the avoidance of replica predators by groups of fish [6,7]. Other authors have proposed that the Condorcet theorem may be applicable to more sophisticated group decision-making processes, such as house-hunting by honeybee colonies [4] (but see [8,9]). Nevertheless the Condorcet theorem as typically applied makes a very strong simplifying assumption - that all decision-makers are equal in their decision-making abilities. Inhomogeneity in biological systems is the rule, however, both through inter-individual differences but also through variations in the quality of information individuals have available to them, which has an inevitable impact on individual decision accuracy. Results have been derived for the case where individual decision-makers vary in their decision-making ability, both in terms of average decision-maker ability [10] and in terms of optimal rules for combining decisions in inhomogeneous groups by confidence weighting [11]. While such results have gained traction in the human behavioural sciences [12,13], and have been noted by authors writing for an animal behaviour audience [4,14], we argue that their applicability to animal behaviour has not been considered in the detail they deserve. We rectify this omission here, reviewing and generalising the relevant theory. We also consider the crucial questions for animal behaviour - how and under what circumstances should honest integration of decision-maker confidence in animal groups be stable. This perspective is distinct from earlier theoretical and empirical investigations into variability in factors such as energetic need [15], boldness [16], intrinsic leadership [17], and

Trends

Theory as applied to collective decisionmaking by non-human animals frequently assumes that all animals have equal decision-making abilities and access to equal-quality information.

Decision theory shows that the optimal group decision-making strategy is to weight contributions to group decisions according to the decision accuracy or 'subjective confidence' of the contributor.

Human groups have been shown to be able to combine judgements optimally, accounting for variations in subjective confidence.

Collectively deciding animals, particularly groups of cooperative breeders, have sophisticated vocal communication abilities and may provide suitable systems to test theory.

The time taken to reach a decision, or hesitancy, provides a link between optimal individual decision-making and optimal group decision-making, and may easily be evaluated by individuals.

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\mathbf{PR} ARTICLE IN

Trends in Ecology & Evolution

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speed [18], which do not a priori correlate with quality of information about the true state of the world. Our intention is thus to motivate further interest among animal behaviour experimentalists in the communication occurring within groups during group decision-making.

Optimising Group Decisions

Optimal decision theory is concerned with maximisation of expected payoff from decisions or, equivalently, minimisation of expected loss. The expected loss is an economic concept that is well known in behavioural biology, for example in the application of signal detection theory to animal behaviour (e.g., [19,20]). As detailed in supplemental information online, minimising the expected loss requires that the prior probabilities of different states of the world are taken into account, as well as the costs and benefits of different decision outcomes, such as true positives or false negatives, under each of these states. An optimal decision-maker minimises expected loss, everything else being equal.

If the decision-maker is a group, then the expected accuracy is a function of the accuracies of all group members, whose contributions to the group decision may be weighted in some way (Box 1). Assuming that individuals cannot change how good they are at making decisions (their accuracies), group decision performance may still be improved by weighting their contributions in an appropriate manner (Box 2). Mathematically there are two equivalent scenarios: an individual signals the weight their vote should have, or groupmates weight it when integrating the votes of their fellow group members. In the following and in the supplemental information online we discuss the derivation, without loss of generality, as if individuals may seek optimally to weight their contribution to the group decision by choosing a weighting rule that minimises the group's expected loss from decisions. In the concluding section we return to which of the two scenarios is more likely under different biological conditions.

When Confidence-Weighting Pays

Confidence-weighting clearly requires additional behavioural and communication machinery beyond simple communication of individual decisions, and this will be costly. To determine when confidence-weighting (see Confidence-weighted vote) will be selectively advantageous it is necessary to consider when it will have the greatest benefits. Reasoning about this is fairly straightforward. In smaller groups the wisdom-of-the-crowd effect is relatively weak, leaving greater potential for group accuracy to be improved by the most accurate individual decision-makers dominating the group [21]. When group members tend to vary widely in their decision accuracy there is again more potential for improvement at the group level by privileging the contributions of the more-accurate members to the group decision. In addition, increasing

Box 1. Group Consensus from Weighted Votes

We can define the consensus decision of a group, reached by combining the individual decisions of constituent group members, as:

$$H(x) = \sum_{i} \alpha_{i} h_{i}(x)$$

where h_i is the decision of the *i*th group member as to whether the state of the world is 'positive' or 'negative' (i.e., $h_i \in \{-1, +1\}$, and α_i is a weight that individual puts on their decision (Box 2). In other words, the decision of a group is a weighted sum of the decisions of its constituent members. Note that positive and negative are simply arbitrary labels we assign to the two possible states of the world, such as predator present and predator absent. We define the correct classification $c(x) \in \{-1, +1\}$ to be -1 if the state of the world is negative, and +1 otherwise, and the hypothesis of a group, H(x) < 0 or H(x) > 0, to indicate their belief about the state of the world (negative or positive respectively); thus the decision of the group is given by the sign of Equation I. The expected accuracy of the group is simply the probability that the sign of Equation I equals the sign of the true state of the world c(x), or E(accuracy) = P(c(x)H(x) > 0).[II]

[I]

In addition, note that the computation of the group decision need not be centralised; Equation I can be computed independently by all members of a group who are communicating with each other.

Glossary

Accuracy: the probability that a decision-maker will make a correct response. If error costs are the same regardless of the true state of the world, then expected accuracy across states of the world should be optimised. However, if error costs differ then optimal accuracies for different states of the world should differ (see signal detection theory). Condorcet vote: a decision in which a group consensus decision is determined by a simple majority vote (at least half of the decision-making population) (see confidence-weighted vote).

Confidence-weighted vote: a decision in which a group consensus decision is determined by integrating the individual decisions of group members, weighted by their subjective confidence. Confidenceweighted votes can be determined by a submajority (less than half of the decision-making population) (see Condorcet vote).

Consensus decision: a group decision in which all group members prefer to implement the same decision. For example, the response to possible predator sightings by a foraging group could be considered a consensus decision because if a predator is absent all members would rather forage than flee and abandon foraging opportunities to groupmates, whereas if a predator is present all members would rather remain with the group to minimise individual predation risk.

Correct decision: in a binary decision, either a true positive or true negative.

Drift-diffusion model (DDM): a

statistically optimal decision-making model that optimises the compromise between decision speed and accuracy (Box 3).

Error costs: costs arising from correct responses and error responses under different states of the world, where an error response is an incorrect decision outcome; in a binary decision either a false negative or a false positive. An optimal decision-maker seeks to minimise expected cost, everything else being equal (see signal detection theory).

Error rate: the probability of a decision-maker making an incorrect response (1 - accuracy).

Trends in Ecology & Evolution

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the mean of the accuracy distribution of the group members reduces the improvements that are possible from optimal weighting because of the rapid increase in group accuracy as individual decision accuracy increases under the simple Condorcet jury scheme (e.g., [3]), limiting the potential for further improvement by weighting votes.

The above reasoning shows that situations in which small groups of relatively poorly informed individuals share information, and where there is variation in either individual decision-making ability or access to information, should prove particularly suitable for evaluating the theory presented here. Existing models of anti-predator vigilance, for example, assume that one or few individuals are well-informed about the approach of a predator [22]. Earlier authors have adapted the theory we present here but applied it instead to individuals weighting cues by their accuracy in a social learning and decision-making context [14]. These authors suppose that when multiple individuals receive the same stimulus then observations will be correlated rather than independent, and opinion-pooling will not be effective [14]. However, we argue that even if multiple individuals independently applied signal detection theory, would still lead to independent observations that could be combined to improve overall group accuracy.

Implementing Confidence-Weighting

How should individuals assess and communicate the quality of their own decision-making? In the simplest case individuals may be assumed to have access to their own decision accuracy, defined as probability of correctly identifying the true state of the world. This accuracy may optionally be conditioned on the state of the world when there are asymmetric costs from errors in each state of the world, for example if the cost of failing to detect a predator is high compared with detecting a predator that is not actually there, or when different states of the world are not equally likely, such as when the prior probability of a predator being present is much lower than the probability that it is absent. Individuals could estimate their accuracy over several observations in a frequentist or even, if armed with an appropriate prior, Bayesian manner, provided that they could also eventually observe the true state of the world. This may be possible during development, when juveniles for example may not contribute to group decisions but may represent an internal decision and then compare that against the eventual outcome (but see [14] for the subtleties of learning within groups). However, this estimation process could be metabolically costly, and benefits may still be realised by more or less principled heuristics for evaluating certainty in decisions. For example, if individual decision-makers integrate evidence over time according to a drift-diffusion process - a reasonable assumption because this optimises the speed-accuracy trade-off inherent in decision-making - and if evidence quality is variable, then time taken to reach a decision can be used as a proxy for the probability that the decision reached was the correct decision [23] (Box 3). Kepecs and colleagues also found that rats presented with ambiguous stimuli waited longer for rewards in error trials than when presented with unambiguous stimuli [24]. Hesitancy in reaching a decision could readily be evaluated by individuals, and observers, in evaluating the probability of a correct decision.

In simpler decision scenarios, while it is somewhat complex to derive the optimal weighting rule from individual accuracy (see Figure I in Box 2), benefits may still be had by implementing simpler confidence-weighting heuristics. For example, even a simple linear weighting scheme would provide benefits over no weighting at all. Similarly there is no requirement for negative confidence weightings (see Figure I in Box 2), which may arise for asymmetric but not for symmetric **error costs** (see Supplemental Information); any affine transformation of vote weightings, adding to and multiplying by the same constants, will leave the group vote unchanged.

Error response: an incorrect decision outcome; in a binary decision either a false negative or false positive.

False negative: failure to detect a positive signal, such as failing to detect a predator that is present. Also referred to as a 'miss' in signal detection theory.

False positive: erroneous detection of a positive signal, such as detecting a predator when none is present. Also referred to as a false alarm in signal detection theory. Log-odds ratio: the logarithm of the decision accuracy divided by decision error rate; can be calculated based on evidence accumulated and elapsed decision time for a driftdiffusion model decision-maker (Box 3)

Signal detection theory: theory prescribing how to set decision criteria to minimise expected error costs (see Supplemental Information). Simple majority decision: a consensus decision reached based on the decisions of at least half the group members, as in a Condorcet vote.

Subjective confidence: a measure related to the statistical confidence an individual has in their own decision, or that other individuals have in the decisions of a focal individual. Optimally defined as the log-odds ratio when used in a confidence-weighted voting scheme. Submajority decision: a consensus decision reached based on the decisions of less than half the group members: this can occur under a confidence-weighted voting scheme (Boxes 1 and 2) when a minority of group members have sufficiently high subjective confidence.

True negative: correct detection of a negative signal, such as not detecting a predator when none is present. Also referred to as a 'correct rejection' in signal detection theory.

True positive: correct detection of a positive signal, such as detecting a predator that is present. Also referred to as a 'hit' in signal detection theory.

Trends in Ecology & Evolution

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Box 2. Optimal Confidence-Weighting of Votes

If individuals can evaluate their individual decision accuracy, then an optimal weighting for their contribution to the group decision (Box 1) can be derived [26,52]. If the expected decision accuracy of individual *i* is a_i , then as shown in the supplemental information online this optimal weighting is

$$x_i^* \propto \sim \ln\left(\frac{a_i}{1-a_i}\right),$$

which is the well-known optimal weighting rule from decision theory [26] and machine learning [52]. This optimal confidence-weighting is illustrated in Figure I.

Equation I is optimal under the assumption that the costs of errors and correct classifications are the same under both possible states of the world, as shown in the supplemental information online. However, in realistic decisions the consequences of errors can be asymmetric; failing to detect a predator is far more costly than stopping foraging to run away from a non-existent predator, for example. As also shown in the supplemental information online a more general form of Equation I can be derived when this assumption is relaxed.



Trends in Ecology & Evolution

Figure I. Optimal Confidence-Weighting. Optimal confidence-weighting parameter α^* as a function of individual decision-accuracy *a* based on Equation I. Note that the contribution of an individual to the group decision should be negatively weighted if its decision accuracy is less than chance (1/2). Note, however, that the overall expected accuracy should not fall below 1/2 for the special case of equal costs for errors under positive and negative states of the world, because if it did the decision-makers could merely reverse their decisions to improve their overall expected accuracy, and thus reduce their expected loss.

Optimal Confidence-Weighting in Humans

To date, tests of the theory have been limited to groups of humans whose highly developed communication and cooperation abilities are obviously sufficient to signal and integrate confidence in reaching a **consensus decision**. A classic study considers group signal detection tasks in groups of up to seven human subjects, studying the deviation from statistically optimal group decision-making as a function of group size [25]. The authors' ideal model, which also improves over Condorcet voting, assumes that individuals combine weighted estimates of a quantity and compare the aggregate value against an optimal decision criterion to determine a binary decision outcome. This is in contrast to optimal combination of the individual weighted binary votes, which has lower communication requirements, and hence their ideal weighting rule differs from that presented here (Box 2). More recently studies have focussed on dyadic interactions in which individuals are assumed to share a nonlinear function of their estimated accuracy [12,13]. For groups of size two this 'maximum-confidence-slating' algorithm is equivalent to the algorithm presented here. Note that communicating misleading **subjective confidences** can lead to worse decisions by groups than by individuals [13]; this result should not apply to our argument where we assume that individuals are able correctly to estimate their

TREE 2261 No. of Pages 10

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Trends in Ecology & Evolution

own or their groupmates' confidence. Subsequently, drawing inspiration from [26], the optimal weighting rule presented here for symmetric costs of errors (Box 2) has been applied to *post hoc* virtual groups of clinicians for medical diagnoses, resulting in an improvement in group diagnosis accuracy [27].

Confidence-Weighting in Non-Human Animals

We argue that collective motion, and vocal communication among cooperative breeders, may prove fruitful avenues for empirical investigation in non-human animals. In cooperative transportation by ants, a recent model has been advanced by which sharing of confidence may improve transportation efficiency [28]; note, however, that in this model, unlike ours, individuals do not vary in their information nor in their ability to process it, hence this model does not correspond to ours. In collective motion, an influential model of target selection by mixtures of informed and uninformed individuals shows how an informed minority can guide an uninformed majority to their preferred target [29]. A key parameter in this model is the relative weight individuals place on their preferred target vector and their desire to remain in proximity to and aligned with their groupmates. This is similar to hesitancy in our proposal above (Box 3), because an individual with weak information about where to go could down-weight its preferred target vector, thereby taking more account of the preferred directions of neighbouring groupmates. While the theory presented here is optimal for binary decisions, further theoretical consideration should be given to optimal confidence-weighting mechanisms for continuous or multi-hypothesis decisions.

Selective Pressures on Confidence-Weighting Mechanisms

What mechanisms should groups use to weight individual decisions? If the individuals within the group in question have sufficiently aligned fitness interests, then they may experience selection

Box 3. Optimal Confidence-Weighting from Optimal Individual Decisions

Statistically optimal binary decision-making, that gives the best possible compromise between speed and accuracy of decision-making, can be realised by individuals using the **drift-diffusion model (DDM)** of decision-making [51] $\dot{x} = \mu + \sigma \eta$ [1]

where \dot{x} is the rate of change over time of a decision variable x, which changes under a constant drift μ but also diffuses under a (white-noise) Wiener process η with standard deviation σ and mean 0. The equal evidence point is x = 0, and evidence typically accumulates until a positive or negative decision threshold is reached. Thus the DDM models evidence accumulation as a process of Brownian motion along a line with a constant tendency μ , that is proportional to stimulus signal to move towards the correct decision boundary, and a constant standard deviation σ , that is proportional to stimulus noise. The DDM achieves the minimum possible expected decision time for a decision with a desired expected **error rate**, achieved by varying the decision thresholds. The DDM can be applied to many problems of animal behaviour, for example, predator vigilance during foraging [20].

It can be shown [23] that the **log-odds ratio** that a decision is correct given the signal (μ) is positive

$P(\langle$	$\mu\rangle >$	0 x(t))
$P(\langle \rangle)$	$ \mu\rangle < 0$	0 x(t))

[11]

[[]]]

can be easily derived for the DDM (see supplemental information online). Here $P(\langle \mu \rangle > 0|x(t))$, for example, is the probability that the estimated sign of the drift coefficient, representing the decision, is positive, given the value of the decision variable x at time t.

If information quality is variable, so multiple possible absolute values of μ might be experienced by a decision-maker, then the log-odds ratio is a function of the value of the decision variable x over time (Figure I).

The log-odds ratio of Equation II is, of course, exactly the same as the optimal weighting rule of Equation I in Box 2 because we assumed that $\mu > 0$, and therefore

$\log \frac{P(\langle \mu \rangle > 0 x(t))}{P(\langle \mu \rangle > 0 x(t))} = \log \frac{P(\langle \mu \rangle > 0 x(t))}{P(\langle \mu \rangle > 0 x(t))}$	$\frac{P(correct x(t))}{P(correct x(t))} = 10$	a(x,t)	
$P(\langle \mu \rangle < 0 x(t)) = \log P(\langle \mu \rangle < 0 x(t))$	P(error x(t)) = 10	$^{9}1 - a(x,t)$	



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where a (*x*,*t*) is decision accuracy as a function of current decision variable and elapsed decision time. Thus the optimal weighting for an optimal individual decision-maker can be computed and, for a fixed decision criterion, evolves in a simple manner over time (Figure IB).



Figure I. Optimal Confidence-Weighting from Optimal Decision-Making. When the quality of the available information is uncertain a decision-maker using the statistically optimal drift-diffusion decision model (DDM) can calculate the log-odds ratio of being correct based on time *t* since decision commencement, and the observed value of an internal decision variable *X* [23] (A). The log-odds ratio corresponds to the optimal weighting rule based on individual decision accuracy Box 2, Equation I described in the main text, as derived in the supplemental information online. For constant decision variable *X* the relationship between decision time elapsed and log-odds ratio is straightforward (B). For both plots the decision-maker has, with equal probability, one of two drift rates ($\mu_1 = 0.5$ or $\mu_2 = 0.1$), and unit standard deviation σ . For both plots the correct decision is uncorrelated with the drift rate experienced.

to communicate honestly the weighting that they judge their vote should have. Such a situation would be likely in a colony of eusocial insects, for example. However, in unrelated groups individual fitness interests will not usually be aligned with those of groupmates. While it may be in the interests of an individual that the group correctly identifies the presence of a predator, for example, to be able to flee while benefitting from a dilution [30] or confusion effect [31], it could also be in the interests of an individual to cause a foraging group to flee when no predator is present, allowing the signaller free access to abandoned food items. Such kleptoparasitism through manipulative alarm calls is observed between species (e.g., [32,33]), and in an intraspecific context signalling increased confidence in a decision could enable an individual

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to manipulate group members. Hence in such groups confidence-weighting would be less attended to by groupmates [34]. By contrast, inferring the accuracy or reliability of groupmates may be feasible, and because each individual must ultimately determine what they think the





Trends in Ecology & Evolution

Figure 1. Many Cooperative Breeders Exhibit Sophisticated Vocal Communication. As described in the main text, (A) Pied babblers (Turdoides bicolor) negotiate vocally over the sharing of cooperative tasks; (B) green woodhoopoes (Phoeniculus purpureus) use vocalisations to mediate group movement decisions; (C) meerkats (Suricata suricatta) make vigilance decisions based on vocal information from groupmates; and (D) dwarf mongooses (Helogale parvula) assess the need for personal vigilance depending on identity information contained within vocal signals. Photo credits: (A) Andrew Radford, (B) Chris van Rooyen, (C) James Marshall (reproduced from [53] with permission from Princeton University Press), (D) Shannon Benson.

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group has decided on, weighting votes by groupmates according to their perceived accuracy as part of this integration could be a stable strategy.

Testing the Theory in Non-human Animals

For vocal communication in non-human animals (Figure 1) there is good evidence that individuals can alter their responses to anti-predator vocalisations depending on the perceived reliability of groupmates [35,36]. Differences in reliability may arise because of variation in inherent characteristics such as age, dominance status, or individual ability [37,38], the use of false calls for kleptoparasitic purposes as discussed immediately above [39], or as a consequence of external factors such as the height adopted by individuals scanning for dangers as raised guards [40]. In principle, it is therefore plausible that, on hearing calling by multiple individuals, receivers will weight those calls by their perceived reliability when making a decision. In the case of alarm calls, however, there may simply not be enough time to make such nuanced judgements; there will be selection for rapid responses to warnings of danger [20], and individual variation in alarm calls has been shown not to be taken into account by receivers in at least some cases [41]. Perhaps more likely would be weighted judgements in situations where there is more time available for decision-making. For instance, when deciding whether and where to move next, how much vigilance to conduct, and how much to contribute to shared activities. In cooperative vertebrates these decisions are often mediated by vocalisations (movement [42,43]; vigilance [44,45]; negotiation over cooperation [46]), and such vocalisations often carry class- or individual-specific information [37,47]. Future work could therefore profitably use playback experiments to explore how group decisions are affected by variation in reliability in these different contexts.

Relating Accuracy Variation with Variability in Other Traits

In this review we have focussed on the application of decision theory based on variation in individual decision-making ability or quality of evidence. An increasing amount of work has studied variation within animal groups and how this translates to leadership [15–18]. Further work may be undertaken to relate such variability to variation in decision-making quality [48], and the relationship between 'personality' and 'swarm intelligence' has been noted to have received little attention [49]. For example, while leadership in pairs of pigeons may correlate with experience [50], Pettit *et al.* find that in larger flocks it is the faster pigeons who become leaders, even though they are not necessarily the more efficient navigators [18]; however, subsequently they become superior navigators, probably because of increased relative attentiveness during navigation [18]. This may be a feature of decision-making during collective motion where a minimum speed is required because of physiological constraints; where such constraints are uncorrelated with decision-quality they become a confound. Note that variation in subjective variables such as hunger or intrinsic leadership is outside the scope of the theory presented here [15,17] which focusses on honest confidence-weighting either by signallers or signal recipients.

Concluding Remarks

We have argued here that variation in individual decision-making ability in animal groups has received insufficient theoretical attention, and have surveyed relevant decision-theoretic models. We have also considered which species and behaviours may provide the most fertile testinggrounds for such theory, focussing primarily on vocal communications in groups of cooperative breeders. Recently there has been greatly increased attention to within-group variation in a variety of traits relating to group decisions, such as boldness and leadership, to take only two examples; we feel, however, that a quantitative, optimality-based approach to optimising group decisions when individuals vary in their decision-making ability offers a complementary perspective.

In conclusion, group decisions can be improved by even relatively simple strategies for weighting contributions to group decisions according to individual decision accuracies; this

Outstanding Questions

Do animals account for decision reliability when signalling to, or integrating signals from, groupmates?

Does confidence weighting shift from signallers in highly related groups to signal receivers in unrelated groups?

Do animals approximate the optimal confidence-weighting strategy?

What confidence-weighting strategies are optimal or effective for continuous and multihypothesis decisions?

Do animals use hesitancy as a cue for inferring confidence in their own or others' decisions?

Trends in Ecology & Evolution

point may not have been adequately appreciated by researchers into collective animal behaviour before now, and we hope that this Opinion will motivate further empirical and theoretical investigation (see Outstanding Questions).

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Supplemental Information

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