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Risk preference during collective decision making: ant colonies make risk-indifferent collective choices

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The study of how animals respond to risk has had a strong influence on our understanding of animal behaviour. By risk, we refer to a situation where organisms must exploit a resource with an unstable quality. Animals may have different risk preferences: they may be risk seeking (e.g. prefer a gamble of 2 or 4 versus a safe bet of 3), risk averse or risk insensitive. Among invertebrates, bees are the most studied group in terms of risk preference. However, in eusocial insects such as bees and ants, the unit of selection is the colony. Thus, the risk preference of eusocial animals is best understood at the level of the group. More broadly, many group-living animals must make consensus decisions between options with varying risk. However, to our knowledge no study has yet set out to examine risk preference during collective decision making by groups. This study aimed to address this gap. Colonies of the ant *Lasius niger* were given access to two feeders, one offering a fixed 0.55 M sucrose solution and the other alternating every 3 min between 0.1 M and 1.0 M. Colonies almost always (26/28 trials) made a collective decision. While there was a small tendency for the variable feeder to be chosen if it initially offered 1 M sucrose, broadly speaking the fixed or variable feeders were equally likely to be chosen. Ant colonies thus showed risk neutrality during collective foraging decisions. Unexpectedly, and contrary to the classical understanding of pheromone-based collective decision making, the choice of feeder was only very weakly influenced by the initial quality of the variable feeder. We propose that risk preference during collective decision making by groups is a woefully understudied topic, and worthy of future work in both recruitment-based and nonrecruiting decision-making systems.

Animals usually have multiple options open to them in any given situation. Options usually vary in their degree of reliability and profitability, and reliability has a direct influence on the value of an option. Understanding how animals choose between options with different levels of reliability is key to understanding how animals exploit their environment. It is also key to understanding how animals (and humans) manage exploration/exploitation trade-offs (Biesmeijer & Vries, 2001; Cohen, McClure, & Angela, 2007; Mehlhorn et al., 2015). Extensive research on foraging under risk and uncertainty has greatly extended our understanding of how animals make these trade-offs, and handle natural, variable environments. Borrowed from economic theory, the term 'risk' used commonly in foraging theory refers to a situation where the mean quality of a resource is known, but its precise value at any one time is not. A gamble on a six-sided die is thus a risky proposition: the average score is 3, but the precise value on each roll is unknown. Related to this, 'uncertainty' or 'ambiguity' refers to a situation where neither the mean nor the variation is known; a gamble on a die with an unknown number of sides is thus gambling under uncertainty (Trimmer et al., 2011). The study of risk in animal behaviour was effectively inaugurated in 1980 by Caraco et al., who provided a clear empirical demonstration of risk-sensitive foraging (Caraco, Martindale, & Whittam, 1980). They showed that yellow-eyed juncos, *Junco phaeonotus*, under a negative energy budget preferentially chose a risky food option (equal chance of either no seeds or 12 seeds), while birds under a positive energy budget preferred a low-risk option (six seeds with certainty). This work was rapidly followed by a flurry of research, but by the 1990s it was becoming clear that the energy budget-based risk sensitivity paradigm for risk choice did not explain well the growing body of research on risk preference in animals (Kacelnik & Bateson, 1996). Rather, an understanding of how animals perceive and learn about the environment provided a better explanation for how animals in

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general respond to risk. For example, owing to nonlinear perception of sweetness, the difference in sweetness between 0.1 M and 0.2 M may seem greater than the difference between 0.2 M and 0.3 M, and this will affect how the relationship between the two food sources are remembered (for a review, see Kacelnik & El Mouden, 2013). Nevertheless, the ultimate drivers of risk-sensitive behaviour remain controversial.

The large body of knowledge regarding how animals respond to risk consists of hundreds of individual research articles detailing experiments on risk preference in various animals. While a broad array of organisms (including slime-moulds and plants, see Dener, Kacelnik, & Shemesh, 2016; Reid et al., 2016) have been tested (Kacelnik & Bateson, 1996), nectarivores have received particular attention (Perez & Waddington, 1996; Shafir, 2000). This is understandable, as nectarivores are relatively easy to train and test since they make rapid return visits to a feeder, and since the question of risk preference is of particular ecological relevance for them: nectarivores must often make repeated visits to semi-permanent food sources which offer different food qualities and quantities, and replenish at different rates. However, it must be kept in mind that the response to risk of nectarivores and non-nectarivores can be very different (Shafir, 2000). As nectarivores are so appropriate for studying risk preference, it is perhaps unsurprising that tests of risk sensitive foraging in invertebrates have been overwhelmingly carried out on bees. However, in spite of the very large body of work on risk preference in bees, the results are often contradictory and conclusions are controversial: for example, bumblebees have variously reported to be risk averse generally (Real, 1981; Real, Ott, & Silverfine, 1982; Waddington, Allen, & Heinrich, 1981) or risk averse when their honey stores are high and risk seeking after their stores have been drained (Cartar, 1991), or risk indifferent (Waddington, 1995). Honeybees, *Apis mellifera*, have been reported to be risk averse (Shapiro, 2000), risk averse in their dancing rates (Seefeldt & Marco, 2008), risk indifferent (Banschbach & Waddington, 1994; Fülöp & Menzel, 2000; Shapiro, 2000), risk seeking when energy levels are declining but risk averse when energy levels are increasing (Mayack & Naug, 2011), or to show varying risk behaviours depending on perceptual accuracy or whether a zero-reward situation was present (Shafir, Reich, Tsur, Erev, & Lotem, 2008; Shafir, Wiegmann, Smith, & Real, 1999).

Several authors have noted that honeybees and bumblebees represent a special case, as they store food which can buffer against short-term fluctuations from risky choices (Banschbach & Waddington, 1994; Cartar & Dill, 1990). However, honeybees also represent a special case for another reason: they can recruit nestmates to resources using the waggle dance (von Frisch, 1967), and can thus make decentralized, collective decisions as a colony to focus on specific resources (Seeley, 1995). Indeed, honeybees and other eusocial animals are superorganisms, where the unit of selection is the colony, not the individual (Hölldobler & Wilson, 2009; Seeley, 1989). Thus, it is behaviour at the colony level that best represents the preference of eusocial animals. It is therefore very surprising that, to our knowledge, no explicit test of risk preference during collective decision making has ever been carried out. Perhaps closest are two recent studies of decision making under risk by non-neuronal organisms, the slime mould *Physarum polycephalum* (Reid et al., 2016) and the pea plant, *Pisum sativum* (Dener et al., 2016). Decision making by non-neuronal organisms is considered to be similar in many ways to collective decision making by superorganisms such as ants, as both systems are decentralized (Reid, Garnier, Beekman, & Latty, 2015). Pea plants were shown to be risk sensitive, choosing risky substrates when in a poor condition and nonrisky substrates when in a good condition. The slime mould was shown to perform well in a situation analogous to a two-arm bandit situation, in which an actor (in this case the slime mould) must continually choose from two options, with each option having an uncertain payoff, but usually one being on average superior to the other (Bergemann & Valimaki, 2006).

However, two studies on collective decision making did inadvertently test risk preference during collective decision making in ants. Franks et al. (2015) offered colonies of rock ants, *Temnothorax albipennis*) the choice between a fixed-quality mediocre nest and a nest that fluctuated in quality (achieved by removing and replacing a darkening foil cover on the nest). They found that ant colonies seemed to correctly assess the 'average' quality of the fluctuating nest, and choose it if this average was higher than that of the mediocre nest. However, Burns, Sendova-Franks, and Franks (2016) performed an almost identical experiment but using larger distances between the nests, and found that colonies almost invariably (40/41 cases) chose the variable nest quality, even if it was only 'good' for 25% of the time. The striking difference in these results was concluded to be due to a lack of recruitment in Franks et al. (2015), owing to the short distances between the nests. This pair of experiments is very important for the current work, as it shows how the addition of social information and recruitment can result in otherwise rational individual agents (O'Shea-Wheller, Masuda, Sendova-Franks, & Franks, 2017) making irrational collective decisions. This stands in contrast to other situations using the same nest selection decision and a closely related species, where the individual agents are irrational, and fall prey to the decoy effect, but the collective decision is rational and resists this effect (Edwards & Pratt, 2009; Sasaki & Pratt, 2011).

The foraging system of honeybees, along with those of other recruiting eusocial insects such as ants and termites, is a complex adaptive system, or more precisely a complex goal-oriented system (Czaczkes, Grüter, & Ratnieks, 2015). As such, the behaviour of the system cannot be well predicted from the behaviour of the individual units that make it up. Related to this, the behaviour of groups often does not well describe the behaviour of individuals, and vice versa (Pamir et al., 2011). The examples of contrasting individual and collective behaviour in nest site selection given above (Edwards & Pratt, 2009; Sasaki & Pratt, 2011) demonstrate this well.

The lack of information and formal investigation of risk preference during collective decision making represents an important gap in the literature. In this study, we aimed to start closing this gap. We tested the collective preference of colonies of the black garden ant, *Lasius niger*, for either a fixed quality 0.55 M sucrose food source, or a variable food source which alternated between offering 0.1 and 1.0 M sucrose. As mass-recruiting ants such as *L. niger* tend to display symmetry breaking (a clear collective choice tends to emerge between two identical food sources; Beckers, Deneubourg, Goss, & Pasteels, 1990; Price, Grüter, Hughes, & Evison, 2016; Sumpter & Beekman, 2003), we expected colonies to make clear collective choices for one or the other feeder. Such collective decisions are usually thought to arise from positive feedback engendered by the pheromone trail (Beckers et al., 1990; Czaczkes, Salmane, Heinze, & Klampfleuthner, 2016; Dussutour & Nicolis, 2013; Goss, Aron, Deneubourg, & Pasteels, 1989; Sumpter & Beekman, 2003), in which small initial differences between food sources are amplified. One might thus hypothesize that the initial state of the variable feeder (better or worse than the fixed-quality feeder) would predict collective decision making, with ants collectively choosing whichever feeder initially offers the highest reward. However, *L. niger* possesses several negative-feedback mechanisms which may counteract such an effect (Czaczkes, 2014; Czaczkes, Grüter, & Ratnieks, 2013a, 2013b). We thus had no strong initial hypothesis about the collective risk preference of the ant colonies tested.