

## Intransitivity and Contextuality in the Decision Making of Social Insect Colonies

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**Abstract.** Historically, social insects presented researchers with myriad examples of rational behaviour. The ability to make decisions based on a transitive hierarchy of preferences is a cornerstone of rationality. Consequently, models of social insect behaviour often assume social insects act according to fixed decision rules that imply a transitive hierarchy of preferences. However, contextual effects, including the number of options presented and the presence or absence of pheromones, can impair social insects' abilities to behave per their transitive preferences. This paper investigates the conditions where contextual effects cause social insects to display intransitive preferences at the individual and colony levels.

**Keywords:** Social Insect Colonies; Decision Making, Contextuality, Intransitivity, Non-Rational Decision Making, Cyclic Systems

### Intransitivity in Human Decision Making

The idea of a correct manner of thought dates back at least to the time of Aristotle and his exposition of the principles of logic as laid out in the *Organon*. For Aristotle, logic appeared to be a tool for reasoning from true statements to true statements. In the 19<sup>th</sup> Century, logic became a subject in its own right, particularly in mathematics, spawning not one logic, but many distinct logics together with ideas of theory and model. The idea of thought as a tool for achieving goals emerged gradually, particularly within the economics literature. This led gradually to the concept of rationality as a tool for making effective decisions in economics, a tool that enables an agent to make choices leading to the achievement of an economic goal, such as maximizing a utility, maximizing a profit, or minimizing a cost or risk.

One subject area that has received a great deal of attention is preference, which is important in an individual making one choice over another, and indifference, when a choice is made

randomly with equal probability for the alternatives. An important feature of rationality in the determination of preferences is said to be the presence of transitivity [1]. This means that if an agent prefers choice A over choice B, and choice B over choice C, then they will prefer choice A over choice C, regardless of context, order of presentation or the presence of competing attributes. Preferences in which transitivity fails are said to be intransitive and characterized as being irrational or non-rational, and therefore to be avoided or dismissed. In both economic and psychological measurement theory, the existence of transitivity has the status of an axiom, since it is necessary in order that an ordinal scale exist for the observable being measured [2]. Since subjects are living agents and not machines, they are prone to errors and inconsistencies in their decision making. This leads to two forms of transitivity, a strong form (strong transitivity, ST) as depicted in the example above, and a stochastic form (weak stochastic transitivity, WST) where  $x$  is preferred

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over  $y$  if it is chosen more than 50% of the time [2].

There has been much debate in the literature on decision making, whether in economics or psychology, as to whether preferences, as expressed by human agents, are always transitive, hence presumably rational, or intransitive, and therefore irrational, and thus worthy of correction. In general, transitivity was held to be fundamental and universal in decision making (since after all humans were clearly rational in forming their decisions) and thus any intransitivity that appeared in experiments must be due to an error of some form or another, and therefore could be dismissed as a genuine form of human decision making. Tversky [2] was among the first to show that under specific experimental conditions it was possible to demonstrate the occurrence of consistent and predictable intransitivity in certain situations of decision making, for example choosing which of two alternatives to take a gamble on. Anand [3] argued on philosophical grounds that intransitivity need not necessarily be irrational. Butler and Progrebna [4] point out that “Transitivity must hold either if a value attaches to each option without reference to other alternatives (choice-set independence), or if an equivalent value results after comparing and contrasting the attributes of the available choice options”. Bar-Hillel and Margalit [5] presented three different contexts within which intransitivity might meaningfully occur 1) where intransitivity results from application of an ethical or moral choice rule; 2) where intransitivity results from application of an ethical or pragmatic choice rule; 3) where the choice is intrinsically comparative, depending upon multiple competing alternatives. In these contexts, intransitivity presents as a plausible consequence.

Evidence continues to accumulate for the presence of intransitivity in human preferences. In one study [6], consumers were presented with three different scenarios and surveyed on their preferences: 1) a choice of goods without restrictions; 2) a choice of goods with budget restrictions and price changes, and 3) decreased disposable income. Transitivity occurred in only 8% of the sample. Evidence of intransitivity has been observed in neuroimaging studies [7], in the gamble paradigm, with insular activity involved in magnitude judgments while posterior cingulate activity was involved in probability judgments.

Not all authors agree, however. Regenwetter, Dana and Davis-Stober [8] argue that transitivity is a universal phenomenon, and any deviation from transitivity is due to agent or experimental error. They write “We challenge the standard operationalizations of transitive preferences and discuss pervasive methodological problems in the collection, modelling, and analysis of relevant empirical data. For example, violations of weak stochastic transitivity do not imply violations of transitivity of preference. Building on past multidisciplinary work, we use parsimonious mixture models, where the space of permissible preference states is the family of (transitive) strict linear orders. We show that the data from many of the available studies designed to elicit intransitive choice are consistent with transitive preferences.” A related criticism of pair-wise comparison experiments has suggested methodological modifications in order to eliminate the appearance of intransitivity [9]. Intransitivity has been explained through at least two forms of error – random preference, in which preferences are transient at each point in time but vary over time, and context-sensitive preference models, in which choice preferences are influenced by current and prior choice contexts [10]. A test of a particular theory of decision making, regret theory, also failed to show evidence of intransitivity [11].

These arguments all assume some form of error in preference determination and appear to deny the possibility of principled intransitivity. Consider the following simple example. I judge ice cream based on two attributes: taste, and the propensity to cause gastroesophageal reflux. One attribute provides pleasure, the other pain. Consider four types of ice cream together with their attribute ratings (taste, reflux potential): double fudge chocolate (100,100), double chocolate (75,75), chocolate (50,50) and pistachio (25,25). I accept pleasure over pain, but only to a point. If the difference in reflux potential is 50 or less, I choose by taste. If the difference in reflux potential is greater than 50, then I choose so as to minimize pain. This leads to the following preferences: double fudge chocolate > double chocolate, double chocolate > chocolate, chocolate > pistachio, pistachio > double fudge chocolate. These choices are quite rational. If given a choice of two similar reflux inducing choices, I might as well pick the more pleasant as the consequences later will be similar. However, if the difference in subsequent

suffering is sufficiently great, the increase in pleasure is not worth the added pain. Note that my decision is principled. If I based my decision on a single attribute, I would find that the corresponding preference orderings would be dual to one another. Intransitivity occurs here because decisions are based upon two competing attributes which possess incompatible preference orderings.

A different set of preferences will be found if I am presented with three choices simultaneously. For example, given double fudge chocolate, double chocolate, and pistachio, I would choose pistachio, because the first two are guaranteed to cause distress. However, given a choice of double fudge chocolate, chocolate, and pistachio, I would choose chocolate because it balances pleasure and pain. The point is that one cannot determine three choice outcomes from two choice outcomes – the context of the situation matters.

Many authors have provided principled (most often mathematical) arguments for the existence of intransitivity. Formally, transitivity is one of the axioms required to define a concept of order, and hence of ordered sets. As noted previously, the axiom of transitivity is required to ensure that preferences form an ordered set, and thus admit description by an ordinal scale. Mathematically, a (*strict*) *partial order* is a simply a transitive relation  $R$  on a set. It does not require a relationship between arbitrary elements or of an element with itself. Elements  $a, b$  for which  $aRb$  are said to be *comparable*. Elements that have no relationship are called *incomparable*. A *linear* or *total* order requires that any two elements must be comparable. The orders considered in economics and measurement theory are called weak orders [12] and consist of partial orders where incomparability is given by its own relation  $I$  (indifference) and  $I$  is required to be an *equivalence relation* (transitive, reflexive ( $aIa$ ), symmetric ( $aIb$  implies  $bIa$ )). Luce [12] was the first to introduce the concept of a semi-order, which generalizes the concept of a weak order to allow for intransitive indifference relations. Of particular interest are those semi-orders where the ordering is induced by means of a utility function  $u$ , that is  $x \geq y$  iff  $u(x) \geq u(y)$ . Many arguments surround the existence and nature of a utility function  $u$  giving rise to the preference relation (and to the probabilities in WST).

An early analysis of intransitivity from a formal perspective was conducted by Fishburn

[13]. He surveyed a number of models for intransitive preferences in settings such as economic consumer theory, multi-attribute utility theory, game theory, preference between time streams and decision making under risk and uncertainty. He analyzed several candidate utility functions and suggested that transitivity is not essential to ensuring the existence of maximally preferred alternatives in a number of situations. People need not always engage in decision making that invokes transitivity, and reasonably so.

Butler and Progrebna [4] describe the Steinhaus and Trybula paradox in which the probabilities of choices all exceed 50% and yet Weak Stochastic Transitivity (WST) is still violated. They conducted a set of lotteries and observed rates of transitivity and intransitivity, accounting for factors such as noisy variation. They concluded that the Steinhaus-Trybula Paradox, in the setting of multi-attribute risky choice, shows that reliance on transitivity may result in a failure to select the most advantageous lotteries, and thus may not provide the most rational decision strategy. They write: “Results support our conjectures that the cycles reflect latent intransitive preference rather than noisy implementation of transitive preferences.” Moreover, they found that “many typically transitive individuals are the same people who violate transitivity in the circumstances we identify. This suggests neither a transitive nor intransitive ‘core’ utility function can accurately describe preferences over all lotteries a person may encounter. .... in line with a constructed-preference paradigm”. This experiment demonstrated that people use different strategies in different contexts; a strategy which appears rational in one context may not be in a different context. Far from being a liability, this makes human decision adaptable to different circumstances. There is no such thing as a one size fits all, or universal strategy.

Panda [14] examined modifications of rational choice theory in the presence of different degrees of intransitivity. These weaker forms of rationality include quasi-transitive rationality and acyclic rationality. He discusses the consistency of these weaker forms and shows how the results change given bounds on the domain of the utility function.

Klimenko [15] has examined intransitivity in a wide range of settings: economic, psychological, social, game theoretic, thermodynamic, and complex dynamic. His works attempts to provide

a unified framework for studying intransitivity across different contexts and introduces a general measure of intransitivity, the evolutionary intransitivity parameter. He points out that “Human preferences that seem irrational from the perspective of the conventional utility theory, become perfectly logical in the intransitive and relativistic framework suggested here”. He concludes that intransitivity should appear under any of the following conditions: relative comparison criteria, multiple incommensurable comparison criteria, multiple comparison criteria that are known approximately, comparisons of groups of comparable elements.

An interesting formal analysis within the setting of game theory again shows that intransitivity need not be viewed as irrational, and indeed may sometimes be the preferred attribute of a decision strategy. Makowski et al [16] present a simple two player choice game and show that the optimal strategy of one player can only be intransitive while that of the second player may be transitive or intransitive. In a quantum version of the game, it turns out that that there is a certain course of the game where only intransitive strategies are optimal for both players.

It has been suggested that there are significant dynamical homologies between collective intelligence systems such as social insect colonies, and neurobehavioural regulatory systems [17] so that collective intelligence systems might serve as experimental proxies for exploring the dynamics of neurobehavioural systems. In particular, a study of intransitivity in collective intelligence systems might provide insights into the role, if any, that intransitivity might serve in neurobehavioural and psychological systems. Thus, we turn now to a consideration of intransitivity in collective intelligence systems.

### **Intransitivity in Collective Intelligence Systems**

Collective intelligence systems refer to a broad range of complex systems, both natural and artificial, all of which are characterized by the capacity to manifest adaptive, intelligent behavior [18] in the absence of any central authority, control, or planning. They are able to make ecologically salient choices in response to changing environmental conditions or contexts through the collective action of large numbers of lesser agents. The prototypical example of a

collective intelligence system is the social insect colony of which social wasps, bees and ants make up the principal examples [19,20,21]. Collective intelligence architectures have been applied to the design of computational systems, but they will not be considered here. The focus here is on the presence of intransitivity in decision making among wasps, bees and ants, and what is known or conjectured regarding the reasons why such intransitivity occurs. An important question is whether such intransitivity is due merely to random errors in effecting decisions, or whether it represents a systematic or principled aspect of collective decision making.

#### *Intransitive Behaviour in Social Wasps and Bees*

Before considering the phenomenon of collective behaviour, let us first examine that of individual workers. Workers of the wasp species *Vespula germanica* were observed individually searching for food [22]. Two experiments were conducted. In the first experiment, three pairs of foraging runs took place. For the first run of each pair a container of 20 gm of meat was placed in a control location. During the second run the container was displaced by 300, 600 and 900 meters respectively. The food dish remained in the same location for both runs for the control group. Wasps in the experimental group spent more time hovering over the previously learned location and the time taken to locate to displaced food increased with increasing distance. In a second experiment, workers were given a choice between a 20 gm source and an 80 gm source, whose positions were reversed prior to a second trial. For the control group the two sources remained in the same positions between trials. On the initial trial, all of the workers went to the 80 gm food container. On the second trial they went to the 20 gm container.

The authors suggested that the wasps' behaviour was attributable to their use of different transitive hierarchies of preferences during their first and second visits to the meat dishes. During their initial visit, the wasps decided where to land based on the quantity of meat present. The wasps used this information to create a hierarchy of locations. In the wasps' hierarchy, the location with 80 grams was superior to that with less. On their second visit, the wasps used the location-based hierarchy instead of reassessing the amount of available meat. In short, irrelevant contextual information (the location of the meat) was baked into the wasps' use of transitive hierarchies and



consequently produced intransitive behaviour [22].

An early study on preferences in honey bees (*Apis mellifera*) [23] demonstrated the existence of intransitivity in preferences. The author created a set of artificial flowers which varied in height and sucrose concentration, from A (short and weak) to D (long and high). They found that individual workers exhibited a pair-preference ordering of the form  $A > B > C > D < A$ , which clearly violates transitivity. In fact, they found workers which violated weak stochastic transitivity and others that violated strong stochastic transitivity. The author suggested that some workers utilized a comparative approach to evaluating the flowers, assessing along several dimensions, each dimension separately. Interestingly, the author identified workers that appeared to utilize both absolute and comparative approaches to decision making.

More extensive studies have been carried out with worker bees. Workers of *Apis mellifera* were tested to determine whether they were capable of learning a transitive hierarchy. Over several days they were trained on 5 different visual patterns (A, B, C, D, E), presented in pairs, with one pattern reinforced (+) by the presence of sucrose, the other pattern unreinforced (-). The pairs were thus (A+, B-), (B+, C-), (C+, D-), (D+, E-). After training, the bees were then presented with novel unreinforced pairs (A, E) and (B, D). The bees consistently chose A over E, the only pair of stimuli which were not ambiguously reinforced. However, they chose B and D almost equally, showing that the bees did not construct the implied transitive hierarchy  $A > B > C > D > E$ . The worker bees appeared to rely on memory constraints (memory of last experience). Here that would discourage E, and so favour A over E. They also relied on associative strength which analysis showed for the pair (B, D) favoured B. Recency, however, favoured D, which results in more or less equal choices. The failure of transitivity appears to be due to memory constraints rather than contextual effects [24].

Contextual effects may influence transitive preferences among bubble bees. A study examined the impact of different conditioning situations on proboscis extensions by workers of *Bombus terrestris* [25]. Individual workers were exposed separately to linalool, phenylacetaldehyde, and a 50-50 mixture, and responded nearly equally (24%, 23%, 27% respectively). They were then subjected to

discriminant pairs with one odor reinforced, the other unreinforced. When linalool was the rewarded odor, the workers preferentially responded to linalool (27.8%). However, in the symmetric situation in which phenylacetaldehyde was rewarded, the workers showed little response to phenylacetaldehyde (6.7%). The authors suggested that linalool may possess salience for the workers which overrides the effect of the conditioning, thus providing in internal contextual effect.

Many experiments in insects have focused on the *decoy effect*. This refers to a situation in which a subject is presented with two alternatives, neither of which is clearly superior, and a decoy option (an option which is asymmetrically dominated—meaning that it is inferior to (dominated by) one option but not to the other) is then presented. In the absence of the decoy, neither alternative should be preferred. If the decoy effect is present, then in the presence of the decoy the subject will show a preference for the dominating option, in violation of the principle of regularity, which asserts that a preference should not change merely through the introduction of additional (non-preferred) options. The decoy effect was observed in a study of *Apis cerana* (Asian hive bees) [26]. Workers prefer warm (30°C) over cool (10°C) sucrose solutions and concentrated (30% w/w) over dilute (10% w/w). Presented with warm, dilute, and concentrated, cool solutions, the workers prioritized warmth. However, if the temperature difference were decreased then priority shifts to concentration. In the latter situation the addition of a decoy favoring the higher concentration solution (the preferred option) did not affect the choice of the preferred solution but did significantly reduce the choice of the alternate solution, demonstrating a decoy effect on preference.

*Apis mellifera* (honeybees) workers were similarly vulnerable to decoy effects. Workers prefer short over long flowers and high sucrose concentrations over weak. Comparing a medium-length flower containing a high sucrose solution to a short one containing less sucrose, the bees demonstrated no preference. But the introduction of long high sucrose flower made the medium length flower more attractive. Likewise, the appearance of a short, low sucrose flower made the short, moderate sucrose flower more attractive [27]. The bees demonstrated that they did not form a transitive hierarchy of preferences based on the intrinsic value of the flowers or sucrose solutions that they saw.

Instead, they compared their options and determined their relative values. Decoys altered the context within which choices should be made, biasing preferences in favour of the option with which they shared an attribute.

Latty and Trueblood [28] provide a detailed and deep analysis of experiments into the preference choices of bumble bees and honeybees. They argue that flower choice is a complex process involving economic considerations, constancy, choice-set size, innate preferences, and composition, all influenced by attributes such as sex, age, nutritional state, satiation, and experience. These different factors interact with one another; it is difficult to imagine that simplistic (rational) strategies will capture the complexity expressed by these insects. Nature may trade optimality for efficiency or adaptability, so that rationality may be the ideal of economists and mathematicians, but not of nature.

#### *Intransitive Preferences in Individual Ants*

Some of the most detailed and interesting work on decision making among social insects has been carried out with individual workers and colonies of various species of ants, particularly *Temnothorax albipennis*. Workers of *Temnothorax* choose nest sites based upon several characteristics such as level of lighting (dark over bright) and entrance width (narrow over wide). Edward and Pratt [29] presented ants with two nest sites, A (dark with average entrance) and B (bright with narrow entrance). Workers choose either of these sites with equal likelihood. However, when suitable decoys are presented, the symmetry in preference is broken: with decoy A (dark with wide entrance) ants prefer A, while with decoy B (bright with narrow entrance) ants prefer B. This showed that individual workers run afoul of the decoy effect. This result was confirmed in a subsequent experiment [30].

Individual ants are also vulnerable to another class of contextual effects, namely contrast effects. A tenet of Prospect Theory is that humans may assess options relative to some reference point rather than based upon some absolute value. Wendt et al. [31] demonstrated a similar phenomenon among workers of the ant *Lasius niger*. Workers were either fed high or low molarity sucrose for a sustained period. Ants routinely fed high molarity sucrose were less accepting of low molarity sucrose solutions than ants routinely fed low molarity sucrose

regardless of their levels of satiation. The ants appeared not to assess the value of food based on its ability to satiate them but rather compared to alternative food sources, even when the alternative food sources in question were not even present. Food received from other workers within the nest appeared to serve as a reference value. The authors showed that this was primarily a cognitive rather than a sensory phenomenon.

Human judgments are frequently influenced by extraneous factors such as the presence of labels. For example, the same wine can be placed in bottles labelled with different prices, and humans will often choose the pricier over the less expensive. A similar phenomenon has been observed in workers of *Lasius niger*. When allowed to choose between high-quality food associated with a low-quality odour or low-quality food with a high-quality odour, workers always selected the high-quality odour despite previous experience with both food sources [32]. Wendt and Czaczkes [33] confirmed these results, showing that *Lasius niger* workers spent more time eating a medium-quality food source if it smelled of high-quality food than if it was unscented. By overvaluing medium-quality food that smelled high-quality, the ants showed that they based their sense of food quality on contextual information provided by smell, which suggests that they could form transitive hierarchies of food preference based on smell alone. However, ants also spent twice as long eating medium-quality food that smelled of low-quality than medium-quality food that smelled medium-quality. In short, smell gave them expectations about food quality, but food quality ultimately played a role in the time ants spent eating. Therefore, the ants' behaviour could not be explained exclusively by reliance on a transitive hierarchy of food smells. Instead, the presentation of low-quality odour directed ants to compare the medium quality food they tasted to the low-quality food they expected. That is to say, the ants' perception of the choice set's composition (a contextual effect) influenced the amount of time they spent feeding and caused them to overvalue medium-quality food relative to its placement on a transitive hierarchy [33].

Contextual effects have also been demonstrated in the movements of ants [34]. *Atta insularis* workers were allowed to escape from a cell using either of two symmetrically placed exits. In the absence of external factors, the workers chose the exits with equal

probability. However, in the presence of an alarm pheromone, workers broke symmetry and preferentially exited from only one of the exits. The choice of exit appeared to be random and independent of the spatial distribution of workers within the enclosure at the time of release of the alarm.

#### *Intransitive Behaviour in Ant Colonies*

The studies presented in the previous sections have all dealt with decision making by *individual* workers within a social insect colony. However, the most interesting studies involve decision making by the colonies themselves, what is called *collective intelligence*. As has been noted above, individual workers are capable of complex decision making, taking account of a potentially large number of factors, and integrating those assessments into a single choice. Often those choices (or the preference probabilities) violate one or more of the principles of rational thought. However, we have also seen that for agents living in the natural world, outside of a laboratory, restrictions of decision making to only rational strategies may not provide the resilience, adaptability, and robustness necessary for survival. The concept of a naturally occurring computational system (NOCS) [35,36] was proposed many years ago to make explicit the distinction between decision making which must be carried out by a living agent in a complex environment, with imperfect knowledge and on the fly, and the idealized agents presented in mathematics, economics, philosophy, or cognitive psychology, which live in simplistic, unchanging environments, have perfect information and have infinite time to examine every possible alternative, and select out only the best according to some arbitrary criterion (usually a fantasized utility function or fitness or truth valuation). Instead, it was argued that NOCS utilize decision strategies that are *good enough*, that achieve some immediate ecological function or goal, in the moment, and then move on to the next task or challenge. Resilience, robustness and adaptability, are far more important than some ideal of optimality [35,36].

Individual workers utilize decision making strategies that manifest some of the features of resilience, robustness, and adaptability, and so often have the appearance of being non-rational. The term non-rational is preferred to irrational as the latter suggests some kind of error or flaw or illness, whereas non-rational simply suggests a normative decision strategy which simply does

not conform to the standards of (idealized) rationality. It then becomes an interesting question to ask whether decision making at the collective level, at the level of the colony itself, is different from that of the individual workers and whether it might offer to the collective an advantage not accorded to the individual. It is important to understand that by collective intelligence one does not simply mean the sum of decisions of the individual workers treated in isolation to one another. That certainly is more typical of collective actions by humans, especially in crowds and mobs. Collective intelligence refers to decision making at the collective level that *emerges* from interactions between the workers of the colony among themselves and with their environment, that *transcends* the abilities of individual workers, which is more than simply the sum of the parts, that is reproducible given similar circumstances, and serves the achievement of salient ecological goals by the colony as a whole.

The dynamics of collective intelligence systems (and NOCS generally) is characterized by generativity, transience, emergence, contextuality, openness to the environment, stigmergy, creativity, and symmetry breaking [37-39], among many other properties. Moreover, it has recently been suggested that there are deep dynamical homologies between collective intelligence systems and the neurobehavioural regulatory systems of the human brain, and that the study of collective intelligence systems, particularly social insect colonies, may shed light into neurodynamics [39].

The most detailed study to date of collective decision making was conducted by Franks et al. [40]. They studied nest emigration by colonies of *Temnothorax albipennis*. Emigration to a new site occurs when a so-called quorum threshold of returning recruiting workers is achieved, a form of mass action or democratic choice. They identified several attributes of potential nest sites which the ants appeared to utilize in making a decision including the brightness of the site, its height, and the width of the entrance. They exposed the colony systematically to a range of paired alternatives under forced emigration and observed which alternative was preferred, measured by the probability of the colony migrating to that site by the end of the day. They showed that the colony appeared to express transitivity in its preference hierarchy. Moreover, following a detailed analysis of the preference hierarchy, they determined that the



colony appeared to use a weighted additive strategy, a sophisticated strategy that can be difficult even for humans [40].

In their study of the decoy effect, Edwards and Pratt [29] subjected the colony as a whole to the same set of alternatives and decoys that were presented to the individual workers. Unlike its workers, decisions at the colony level evaded falling prey to the decoy effect. The fact that colony level decisions arise from interactions between workers rather than simply summing worker preferences may provide a mechanism by which the colony is able to effect more rational decisions which its workers cannot on their own.

However, the situation is nuanced. The ability of the colony to utilize a rational strategy depends upon contextual factors. For example, a study of foraging by *Myrmica rubra* [41] found that modifying the available choice set by increasing the number of nest entrances from one to two resulted in worse foraging outcomes. In nests with one entrance, *Myrmica rubra* ants leaving the nest navigated to the more abundant of two food sources 43% of the time compared to 34% of the time in the two-entrance condition. The poorer performance appeared to be due to fact that these colonies use pheromone to recruit to foraging trails, and pheromone must be dispersed over a wider region in the two-entrance case compared to the single entrance case.

In a study of nest selection in *Temnothorax albipennis* [42], researchers forced ants to migrate from a high-quality nest and to choose between a mediocre and a poor nest site. The ants universally moved to the mediocre site. However, if ants were exposed to an alternative nest site prior to being forced to emigrate, and then later forced to choose between the familiar alternative and an unfamiliar alternative, they showed an aversion for the familiar alternative, even when that led to the choice of a poorer site. The intensity of this aversion was influenced not just by the quality of the alternative but also by the quality of the home nest. For example, if the home nest was of mediocre quality the aversion appeared to disappear. The authors used formal modeling to show that these results did not necessarily imply that workers used comparative strategies to effect decisions, as often assumed to be the cause of non-rational decisions. Comparative strategies might manifest at the colony level, but individual workers could use absolute strategies combined with threshold-based decision rules. The authors thus

demonstrated how an experience-dependent, flexible strategy can emerge at the global level from a fixed-threshold strategy at the local level.

O'Shea-Wheller et al. [43] observed that individual workers appear to manifest a heterogeneous range of decision thresholds which manifest in the duration that they spend in a potential nest site. Overall, the duration of time spent in an alternative site varied directly with nest quality, but the actual times spent varied from individual to individual. They then carried out a computational simulation and showed that the presence of heterogeneous thresholds allowed the colony to effect optimal, self-organized emigration decisions without the need for direct comparisons at the local level.

Doran et al. confirmed those results [44]. In their study of nest selection in ants they found the tendency of a colony to move was not based on the value of alternate sites in some abstract sense. Instead, colonies assessed nest-sites based on the potential fitness benefit of moving. In an already good nest site, no migration would convey significant fitness benefits. But, for a colony recently made homeless, any nest would do. Therefore, while colonies compared the mediocre nest to the good one, they compared the poor nest to nothing at all. Ultimately, because a nest site's value to an ant colony was context-dependent, two nests assessed under different conditions were not evaluated on the same transitive hierarchy. Furthermore, they were able to show that flexibility was not entirely relegated to the colony, but individual workers were also able to modify their response through changes in recruitment speed.

Healey and Pratt [45] placed *Temnothorax curvispinosus* colonies in either high- or low-quality nest sites for 8 weeks. They then measured the time taken to recruit to a mediocre site. Contrary to expectation, they found that colonies moved more rapidly after living in a good nest than in a poor nest. Life within a poor nest may affect the size and well-being of the workers within the nest, resulting in a slower response but provided evidence for an urgency hypothesis, which suggests that the loss of a nest was more dramatic for colonies housed in good nests, causing workers to lower their acceptance thresholds further than those of ants housed in poor nests.

Franks et al [46] further analyzed the scenario of [42]. As before, when workers in a colony were exposed to an alternative nest site of lower



quality than their own and then forced to emigrate facing the familiar alternative and a novel alternative of similar quality, they avoided the familiar site and opted for the novel. They thus broke what should have been preference symmetry. However, if presented with familiar and novel high-quality sites, they maintained symmetry. The experiment was repeated and just prior to emigration, all pheromone marks were removed, and landscape cues were reoriented. Following this intervention, symmetry was restored in the case of low-quality alternatives. This showed that workers are capable of assessing and retaining information about potential nest sites using pheromones and landmark cues.

Stroeymeyt et al [47] repeated their experiment on nest emigration but examined the impact of seasonality on performance. They showed that the aversion to the familiar alternative site was present during the summer months, but during the winter months preference reversed, now favouring the familiar alternative. This appeared to be due to the presence of a seasonal pheromone which is secreted during the summer months and enhances the aversive response to the familiar site. Location factors did not appear to play a role. The presence of such a pheromone interfered with any ability of individual workers to form independent judgments, which could increase error rates, but at the same time increased cohesion and information transfer among the workers.

The study of decision making among social insects has proven to be a fruitful subject matter for the application of sophisticated mathematical and computational models [37,38], particularly in the past 20 years. However, formal research into the role of context in decision making goes back much further. An early paper by Houston [48] used formal analysis of a mathematical model of foraging to show that the fitness value of any food item was contextual rather than absolute, dependent on its alternatives and its probability of being foraged. He argued that it was unlikely that natural selection could thus assign an absolute fitness value to each food option. Even if rationality was possible, it would perform sub optimally compared to context-dependent decision-making methods that violated a form of stochastic transitivity [50].

These ideas are supported by the work of Varon et al [49] on colonies of *Atta cephalotes*.

*Atta cephalotes* colonies modified their food preferences in response to the variable abundance of potential food sources. On coffee farms, where 85% of the foliage was composed of coffee leaves, *Atta* workers derived only a minority of their resources from coffee and collected poro leaves instead. Under lab conditions, where more than 25% of the available biomass was from poro trees, the *Atta* workers neglected it. In other words, ants at the colony level favoured whatever leaf was less abundant, demonstrating that no leaf was assigned a constant fitness value for inclusion in a transitive hierarchy. Instead, foraging behaviour at the colony level was context-dependent [49].

Nicolis et al [50] pointed out that collective intelligence systems often rely upon some form of positive feedback in order to effect their decision making. Using a combination of formal and computational modeling and analysis, they were able to show generically that the probability of choosing the best out of a choice of  $n$  options depended crucially upon the strength of the feedback. There is an optimal level of feedback which maximizes this probability, and this optimal value of feedback depends upon the number of options. Thus, changes in the number of options presented to a collective intelligence system could give rise to the appearance of non-rational decisions.

Sasaki et al [51] studied decision making by colonies of *Temnothorax rugatulus*. Through direct experimental observation and computational modeling, they studied the ability of colonies versus individuals to choose between nests having varying degrees of difference among them. Experimentally they showed that colonies outperform individuals when the degree of difference is small so that discrimination is difficult. When the degree of difference is large, and so discrimination is easy, individuals outperform colonies which are more prone to errors in such circumstances. They developed a computational model, which, similar to [48], which emphasizes the role of positive feedback. They showed that positive feedback enabled the colony to integrate information from individuals and enhance the discrimination between fine differences. However, when the differences are large, positive feedback can lock the colony into choices which ultimately turn out to be suboptimal.

### Contextuality

The importance of context in probability

theory was noted even by Kolmogorov [52] when he developed his mathematical formulation of the laws and structure of probability theory. It is impossible, in general, to form a joint distribution from arbitrary random variables from which the original distributions can be obtained as marginals of the joint distribution. The conditions under which such a joint distribution may be formed have been known for decades [53], but this has mostly been ignored. Moreover, making the same measurement in different contexts does not imply that the same random variables (probability distributions of measured values) have been obtained. Different contexts may result in different random variables for the same measurement process [54]. Failing to take such contextuality into account can lead to erroneous conclusions. Dzhaferov and colleagues have developed a model of this situation, termed *Contextuality by Default*. A concise summary of the Contextuality by Default model is given in [82]. Following the notation in that paper, each random variable is associated with the quantity,  $q$ , being measured and the context,  $a$ , within which the measurement is made, and denoted,  $R_q^a$ . Consider two measurements,  $q, q'$ , and two contexts,  $a, b$ . For a fixed context,  $a$ , the pair  $R_q^a, R_{q'}^a$  is termed *bunch*, representing the collection of measurements associated with a specific context. It is reasonable to believe that such a pair is jointly distributed. For a fixed measurement,  $q$ , the pair  $R_q^a, R_q^b$  is termed a *connection* for  $q$ .

The most basic form of contextuality occurs when no joint distribution can be found for a connection. In such a case, they are said to be *inconsistently connected*. This is the situation of Contextuality by Default. Dzhaferov considers this to be the most trivial form of contextuality because it is so ubiquitous. Dzhaferov has developed a more restricted notion of contextuality, in line with contextuality in physics. He considers couplings between bunches. For example, given two bunches,  $R_q^a, R_{q'}^a$  and  $R_q^b, R_{q'}^b$ , a coupling is a set of jointly distributed random variables  $(A, B, X, Y)$ , subject to certain constraints, such that  $(A, B)$  is distributed as  $R_q^a, R_{q'}^a$  and  $(X, Y)$  is distributed as  $R_q^b, R_{q'}^b$ . The constraints involve  $A, X$  and  $B, Y$ , which correspond to measurements of  $q$  and  $q'$ , respectively. A measurement,  $q$ , is considered to be *context-independent* if, among all couplings

$(A, B, X, Y)$ , we have  $Pr(A \neq X) = 0$ . It can be shown that such a coupling may not exist even if the system is consistently connected.

Now, considering all couplings  $(A, X)$  for just the connection  $R_q^a, R_{q'}^a$ , the minimal value  $m'$  can be found for  $Pr(A \neq X)$ . Then, considering the global coupling  $(A, B, X, Y)$ , the minimal value  $m$  for  $Pr(A \neq X)$  can again be found. If  $m = m'$ , the system is non-contextual, and if  $m > m'$ , then the system is contextual. This form of contextuality is analogous to that found in physics.

The discovery that contextuality occurs even in fundamental physical systems was a seismic shock to physicists in the last century. It has led to endless speculation about the nature of reality, but in actuality it merely was a recognition that contextuality is a fundamental feature of nature. However, the probability theory of quantum mechanics is non-Kolmogorov, founded upon complex numbers rather than real numbers as in Kolmogorov theory. Khrennikov [56] has developed a theory of non-Kolmogorov probability and applied it outside the realm of quantum physics. Dzhaferov's model, on the other hand, is framed within Kolmogorov probability theory, but makes explicit the connections between random variables and their contexts.

The non-Kolmogorov structure of quantum mechanics leads to phenomena which cannot occur within classical Kolmogorov probability theory. This is best seen using the inequalities of Bell, which point to the existence of correlations between random variables which are greater than those possible within a classical Kolmogorov theory. Dzhaferov and Kujala have developed an analogue of the Bell inequalities for use within the Contextuality by Default model, and have demonstrated the existence of these supra-classical correlations in psychological settings [57,58]. In particular they focus upon a specific set of psychological measurements termed cyclic systems.

### Contextuality and Cyclic Systems

The random variables considered by Dzhaferov (and used in formulating the Bell inequalities in quantum mechanics) form what is termed a cyclic system. A cyclic system of rank  $n$  consists of  $n$  bunches based upon  $n$  quantities and  $n$  contexts and arranged in the following manner

$$(R^1_1, R^1_n), (R^2_1, R^2_2), (R^3_2, R^3_3), (R^4_3, R^4_4), \dots (R^{n-1}_{n-1}, R^n_n)$$

For example, a cyclic 4 system has the form

$$\begin{bmatrix} R^1_1 & 0 & 0 & R^1_4 \\ R^2_1 & R^2_2 & 0 & 0 \\ 0 & R^3_2 & R^3_3 & 0 \\ 0 & 0 & R^4_3 & R^4_4 \end{bmatrix}$$

which can also be written in the form

$$R^2_1 - R^2_2 - R^3_2 - R^3_3 - R^4_3 - R^4_4 - R^1_4 - R^1_1$$

In [55] it is shown that a cyclic system of the form

$$V_1 \text{ --- } W_2 \text{ --- } V_2 \text{ --- } W_3 \text{ --- } \dots \text{ --- } V_n \text{ --- } W_1$$

is non-contextual if the following inequality holds

$$\Delta C = s_1(\langle V_1 W_2 \rangle, \dots, \langle V_{n-1} W_n \rangle, \langle V_n W_1 \rangle) - (n-2) - \sum_{i=1}^n |\langle V_i \rangle - \langle W_i \rangle| \leq 0,$$

where  $\langle \rangle$  denotes expectation value and  $s_1$  is the maximum over all sums of the form

$$\pm \langle V_1 W_2 \rangle \pm \langle V_2 W_3 \rangle \dots \pm \langle V_{n-1} W_n \rangle \pm \langle V_n W_1 \rangle$$

such that the number of minus signs is odd

### Cyclic Systems in the Current Literature

Cyclic systems form convenient but also ubiquitous settings in which to test for the possibility of quantum-like contextuality in classical systems. As noted above, human decision making is an ideal setting for obtaining cyclic systems. Studies of decision making in collective intelligence systems, especially social insect colonies are another potential source of cyclic systems. Pair-wise comparisons of multiple observables in multiple contexts provide excellent opportunities for creating cyclic systems. Unfortunately, most of the studies of decision making in social insect colonies were not designed with issues of contextuality in mind. Some studies examine multiple observables within a single context

[34]. Others examine a single observable within multiple contexts [31].

Another problem is that in many experiments, the observables form mutually exclusive pairs, even if multiple contexts are involved. For example, Oberhauser et al [32] examined two observables: the marginal probability of an ant moving towards 1.5M sucrose solution (object X) and the marginal probability of an ant moving towards 0.25M sucrose solution (object Y), and two contexts: one where the ants had conflicting information about the location of the 1.5M sucrose solution (context 1) and one where they did not (context 2). The four random variables produced by this combination are seemingly sufficient to form a cyclic system of rank two. However, the two observables are mutually



exclusive, so that the expectation values in the contextuality inequality are all zero, and such systems are non-contextual by definition.

The problem of the mutual exclusivity of observables is fairly widespread [29, 42, 46, 47].

### A Cyclic System of Rank 3

A study of commitment time in *Temnothorax albipennis* ant colonies provides an illustration of a cyclic 3 system [44]. The study's contexts were the alternative nest sites presented, and its observables were the perceived values of the original nest sites. More specifically, the study had the following four objects [44].

$q_1$  = Marginal probability of emigration from a low-quality nest within 6 hours

$q_2$  = Marginal probability of emigration from a mediocre nest within 6 hours

$q_3$  = Marginal probability of emigration from a good nest within 6 hours

$q_4$  = Marginal probability of emigration from an excellent nest within 6 hours

Its four contexts were as follows.

$c_1$  = presence of a low-quality alternative nest

$c_2$  = presence of a mediocre alternative nest

$c_3$  = presence of a good alternative nest

$c_4$  = presence of an excellent alternative nest

On its face, the number of contexts and objects appear sufficient to form a cyclic system of rank four. However, to form a cyclic system, all objects must appear in two bunches and object  $q_4$  only appears in context 4 [52]. Consequently, the cyclic system can only use the objects  $q_1$ ,  $q_2$ , and  $q_3$ . Furthermore,  $c_1$  only contains one object,  $q_1$ . Consequently, the cyclic system can only use the contexts  $c_2$ ,  $c_3$ , and  $c_4$ . Therefore, the bunches for each context have the following joint probability distributions [44].

$$c_2 = q_1 \wedge q_2$$

$$c_3 = q_2 \wedge q_3$$

$$c_4 = q_3 \wedge q_1$$

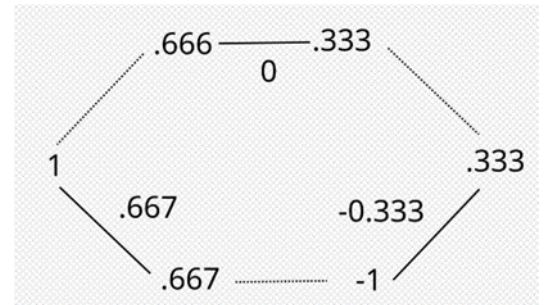
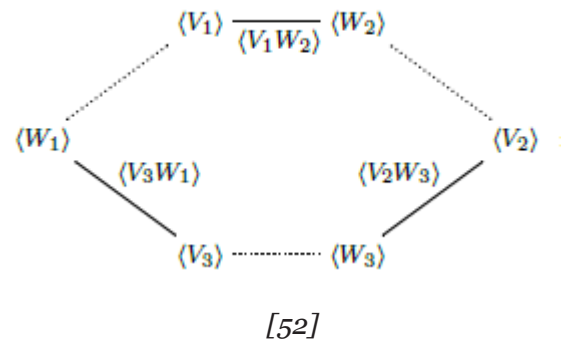
Placing these values into a cyclic system involves the following calculations. Here, the + symbol in the subscripts must act as a stand in for cyclic addition [52].

$$V_i = 2(q_n) - 1$$

$$W_i = 2(q_n) - 1$$

$$V_i W_{i+1} = 4(q_n \wedge q_{n+1}) - 2(q_n) - 2(q_{n+1}) + 1$$

The Cyclic System formed from these values is as follows.



Here we employ the following formula for calculating contextuality in cyclic systems of rank 3.

$$\Delta C = s_1(\langle V_1 W_2 \rangle, \langle V_2 W_3 \rangle, \langle V_3 W_1 \rangle) - 1 - \sum_{i=1}^3 |\langle V_i \rangle - \langle W_i \rangle| \leq 0$$

where

$$s_1(x, y, z) = \max(x + y - z, x - y + z, -x + y + z, -x - y - z).$$

[52]

In our case,  $\Delta C = -1.99$ , showing no sign of contextuality.

## Conclusions

Rationality is generally held to represent the epitome of decision making – logical, optimal, goal achieving, elegant, perfection, especially from a mathematical perspective. However, the exercise of rationality requires conditions that are far removed from those encountered by agents in the natural world, such as perfect knowledge of present and future possibilities, unlimited time, fixed utilities against which to judge outcomes. The natural world is characterized by transience, contextuality, conditionality, openness, incomplete knowledge, indeterminate (or even absent) utilities, a far cry from the conditions for rationality. The decision making of collective intelligence systems such as social insects may not be rational in the strict sense, but it is certainly well adapted to enable them to achieve ecological functionality and goals. After all, social insects have been present on Earth for over 200 million years. If rationality is so essential to success, then how does one account for the evolutionary success of the social insects? The answer may tell us more about the dynamics of human brains than has previously been thought. In particular, the study of decision making in collective intelligence systems provides an ideal setting for study the role of contextuality in decision making generally.

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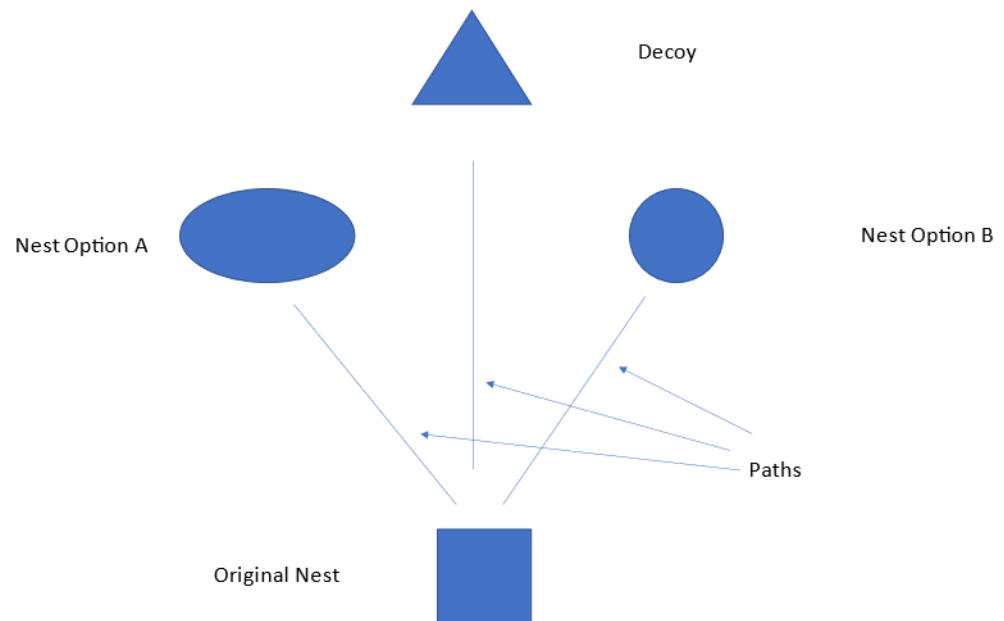
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**Supplementary materials**



**Figure 1.** Cartoon of the general experimental arrangement for decision making in social insect colonies