Seasonality in communication and collective decision-making in ants

N. Stroeymeyt1,2,3,†, C. Jordan1, G. Mayer1, S. Hovsepian1, M. Giurfa2,3 and N. R. Franks1

1School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK
2Centre de Recherches sur la Cognition Animale, Université de Toulouse, Toulouse, France
3Centre de Recherches sur la Cognition Animale, CNRS, Toulouse, France

The ability of animals to adjust their behaviour according to seasonal changes in their ecology is crucial for their fitness. Eusocial insects display strong collective behavioural seasonality, yet the mechanisms underlying such changes are poorly understood. We show that nest preference by emigrating Temnothorax albipennis ant colonies is influenced by a season-specific modulatory pheromone that may help tune decision-making according to seasonal constraints. The modulatory pheromone triggers aversion towards low-quality nests and enhances colony cohesion in summer and autumn, but not after overwintering—in agreement with reports that field colonies split in spring and reunite in summer. Interestingly, we show that the pheromone acts by downgrading the perceived value of marked nests by informed and naive individuals. This contrasts with theories of collective intelligence, stating that accurate collective decision-making requires independent evaluation of options by individuals. The violation of independence highlighted here was accordingly shown to increase error rate during emigrations. However, this is counterbalanced by enhanced cohesion and the transmission of valuable information through the colony. Our results support recent claims that optimal decisions are not necessarily those that maximize accuracy. Other criteria—such as cohesion or reward rate—may be more relevant in animal decision-making.

1. Introduction

Groups of individuals can be surprisingly adept at predicting future events and solving complex problems, and often outperform smart individuals or experts [1–3]. This phenomenon, known as ‘swarm intelligence’ or ‘the wisdom of crowds’, has been extensively studied and inspired many applications in human societies (reviewed in [1,3]). In animals, groups may also exhibit increased cognitive abilities compared with individuals [4]—and this has been particularly well studied in the context of collective decision-making. Many studies have focused on the ability of groups to make more accurate decisions (i.e. to be less error prone) than individuals [3,5–9], and to trade-off speed with accuracy depending on conditions (reviewed in [10]). This overwhelming focus on accuracy may be due to historical reasons. The first argument for collective intelligence was indeed presented in the eighteenth century by the Marquis de Condorcet: in a jury where jury members are independent, unbiased and have a better than random chance of being correct, the majority of jurors are more likely to make an accurate judgement than each individual juror. The assumption of independence underlying Condorcet’s ‘jury theorem’ has sparked a lot of interest and is deemed crucial to ensure collective accuracy [3]; if independence is violated, collective processes can amplify informational biases or propagate initial errors [11,12], and in humans even mild social influence was shown to undermine severely the wisdom of crowds effect [13].

Recent studies have refined the condition of independence in animal collective decision-making, as exemplified by nest-site selection in social insects.

†Present address: Département d’Ecologie et d’Evolution, Université de Lausanne, Lausanne, Switzerland.

Received: 26 November 2013
Accepted: 15 January 2014

Subject Areas:
behaviour, ecology

Keywords:
collective decision-making, accuracy versus cohesion, seasonal polydomy, chemical communication, independence, Temnothorax

Author for correspondence:
N. Stroeymeyt
e-mail: nathalie.stroeymeyt@unil.ch
[8,14]; the well-known ability of honeybee swarms and *Temnothorax* ant colonies to select the best among multiple available sites (reviewed in [15]) is predicted to require both (i) independence among individuals in the evaluation of available options [8] and (ii) interdependence in the form of quality-dependent recruitment to specific sites [8,14] and cross-inhibition between populations of scouts committed to different alternatives [14,16]. Accordingly, evaluation of nest sites has always been assumed to be independent in house-hunting social insects [12,15,17]. Interestingly, the prediction of independent evaluation makes the implicit assumption that house-hunting social insects aim to maximize accuracy—or to achieve an optimal compromise between the speed and accuracy of their decisions [14]. However, recent studies [16,18,19] have questioned the relevance of accuracy in house-hunting, arguing that fitness gains are solely determined by the value of the chosen site and the decision time, independently of whether that site really is the best in the surroundings (i.e. independently of the accuracy of the decision). Emigrating colonies are thus predicted to make value-based rather than accuracy-based decisions, and to manage speed–value trade-offs rather than speed–accuracy trade-offs [16,19]. For example, if the difference between available options is small enough, the benefits of accurately choosing the highest value nest may be negligible and largely outweighed by the concurrent time-costs of a lengthy deliberation process [16,18]. This puts into question whether independent evaluation should always be expected in nest-site selection by social insects. Here, we experimentally investigated whether this condition is satisfied during nest choice by the ant *Temnothorax albipennis*. 

*Temnothorax* ants inhabit fragile natural cavities—such as rotting twigs, hollow acorns and rock crevices—so colonies frequently have to emigrate to a new nest if the conditions are no longer favourable [20]. Many *Temnothorax* species—including *T. albipennis*—are seasonally polydomous, i.e. individual colonies occupy a single or several nest sites, depending on the season [21–23]. This suggests that their decision-making strategy varies seasonally. Accordingly, we investigated the decision-making mechanisms of *T. albipennis* colonies in summer, in autumn and in winter. More specifically, we aimed to identify the mechanisms responsible for the collective aversion towards familiar, low-quality nest sites previously reported in this species, as we suspected it might breach independent evaluation: colonies are known to gather information about available, low-quality nest sites while their own nest is intact, and later to avoid these sites when forced to emigrate [24–26]. We first evaluated the relative importance of positional versus chemical cues in nest-site selection at different times of year, and found that collective aversion towards low-quality nests is mediated by aversive nest-marking chemicals. Certain chemical signals used by *Temnothorax* ants are known to be individual-specific, i.e. they specifically influence the behaviour of the workers that laid them [27–29]. Aversive nest-marking chemicals could therefore constitute either private or social information. In the first scenario, collective aversion would depend on key informed workers leading the decision-making process [30], whereas the second scenario would entail the violation of independent evaluation. To discriminate between these hypotheses, we investigated whether aversive nest-marking chemicals directly influence nest preference by naive groups of workers.

2. Material and methods

Eighty-eight colonies of *T. albipennis* were collected in Dorset, UK, and brought to the laboratory in the University of Bristol, UK. Colonies were kept in large Petri dishes (22 × 22 × 2.2 cm) with Fluon-coated walls and housed in artificial nests consisting of a cardbox perimeter sandwiched between two glass slides (50 × 76 mm), with an internal cavity of 35 × 50 mm, a ceiling height of 1.1 mm and an entrance of 8 × 2 mm. Nest quality was varied by manipulating light levels within nests: bright nests let light in through their top slide, whereas dark nests were covered with cardboard to prevent light from entering the nest cavity. *Temnothorax albipennis* colonies consistently prefer dark over bright nests [31,32] and develop an aversion towards bright nests when housed in a dark nest [24,26]. Indeed, light levels within the nest are used by the ants as a proxy for the number and/or size of openings to the outside environment [31]; a nest with few, small openings (dark nest) is easier to defend and allows better protection from exterior conditions than a nest with many, large openings (bright nest). The experimental bench was located along a large window with no artificial lights in the local vicinity; therefore, colonies were exposed to natural lighting conditions during experiments.

(a) Experiment 1: the relative roles of positional cues and nest-marking chemicals on aversion

To evaluate the relative roles of positional cues and nest-marking chemicals in mediating collective aversion, we induced ant colonies to develop an aversion towards a bright nest site (familiar nest) and measured their preference between that nest and an otherwise identical, but unknown nest (unfamiliar nest) in three conditions (figure 1a): (i) positional cues consistent with nest-marking chemicals (control); (ii) only positional cues present (i.e. nest-marking chemicals removed, removal) and (iii) positional cues conflicting with nest-marking chemicals (exchange).

Collective aversion towards the familiar nest was induced as in previous studies [24,26]: colonies housed in a dark nest were allowed freely to visit and familiarize themselves with a bright nest during one week. Colonies were then induced to emigrate by removing the top glass slide and the cardboard perimeter of the old nest, and their preference between two equidistant nest sites was recorded (see below). In the treatments control and exchange, emigrating colonies could choose between the previously explored, familiar bright nest and an identical, previously unexplored unfamiliar bright nest. In the control, just before the onset of emigration, the familiar nest was picked up and then put back at exactly the same position as during exploration, whereas in the treatment exchange, the positions of the familiar and unfamiliar nest sites were switched (figure 1a). In the treatment removal, the familiar nest was replaced with a clean nest just before the onset of emigration, so colonies had to choose between two identical, unfamiliar bright nest sites, one of which occupied the previous location of the familiar nest (figure 1a).

This experiment was first carried out in January–February 2009 with 24 colonies collected in January 2009 (winter replicate), then replicated with the same design in July–August 2009 with 24 colonies collected in July 2009 (summer replicate). Colonies collected in winter and summer had similar adult population sizes, but winter colonies had more brood (unpaired t-tests, adults: \( t = -0.72, \text{d.f.} = 46, p = 0.48 \); brood: \( t = 5.66, \text{d.f.} = 46, p < 1 \times 10^{-5} \)). In addition, summer colonies were collected at the end of a mating flight, so they still contained reproductive individuals in very low numbers (mean ± s.e.: 4.6 ± 1.2% of the total number of adults).
Figure 1. Experiment 1. (a) Diagram of the experimental set-up (ON: old nest, dark, destroyed after exploration; FN: familiar nest, bright, visited during exploration; UN: unfamiliar nest, bright, never visited prior to emigration). The position of the FN (left or right) was pseudo-randomized between trials. (b,c) Nest preference after 24 h. Nests differed in their position (FP: familiar position, occupied by the FN during exploration; UP: unfamiliar position, on the other side; *p < 0.05 in Friedman test) and in their origin (dotted: previously explored FN; white: previously unexplored UN; n.s.: p > 0.5 in Wilcoxon matched-pairs test). Full squares with horizontal lines, rectangles and whiskers, respectively, represent the median, interquartile range and full range of the proportion of colony items observed in each nest. For each treatment, the data presented for the FP nest is complementary to the data presented for the UP nest (i.e. proportion in FP = 1 – proportion in UP). The dashed line represents expectations under the hypothesis of random choice between nests (*p-values of corresponding median tests are given for each treatment). (d,e) Cohesiveness of colonies under the three conditions for both replicates (Kruskal–Wallis tests; summer: p < 0.00005; winter: p = 0.17). Full squares with horizontal lines, rectangles, whiskers and full circles respectively represent the median, interquartile range, full range or 1.5 × interquartile range, and outliers. Different letters indicate significant differences between treatments (Siegel–Castellan post-hoc tests, p < 0.05).
(b) Experiment 2: do nest-marking chemicals influence naive nest-mates?

Experiment 2 aimed at determining whether the nest-marking chemicals identified in experiment 1 influence the behaviour of naive individuals (i.e. individuals that have not previously visited the familiar nest). Forty colonies were split into two equal halves (colony halves from the same mother colonies will henceforth be referred to as sister half-colonies). Half-colonies housed in a dark nest were allowed to explore an experimental arena for one week (figure 2). During exploration, informed half-colonies could familiarize themselves with an available bright nest site (familiar nest) inside their arena, whereas at the same time naive half-colonies had no nest site to visit. In the control, informed half-colonies were then induced to emigrate and allowed to choose between the familiar nest and an identical, previously unexplored bright nest. In the treatment transfer, familiar nests were removed from the arena of informed half-colonies and introduced into the arena of their naive sister half-colonies at the end of exploration. Naive half-colonies were then immediately induced to emigrate and allowed to choose between the transferred familiar nest and an identical, previously unexplored bright nest. Thus, workers in the control could potentially use both private and social information, as some had previously visited the familiar nest, whereas workers in the treatment transfer could only rely on social information, as none had previously been in contact with any of the new nests. Nest transfers were always made between sister half-colonies to avoid any confounding effects of nest-mate recognition [33].

This experiment was carried out in October–November 2009 with 40 colonies collected in September 2009.

(c) Data collection

During emigrations, we recorded the discovery time (time interval between emigration onset and first entrance into the new site) of both new sites for a random sample of colonies. Additionally, in experiment 2, we counted the number of ants exploring the candidate sites every 5 min during the first hour of emigration. We evaluated the distribution and cohesiveness of the colony 24 h after the onset of emigration by using the following formulae [25]:

$$P_{N1} = \frac{N_1}{N_1 + N_2}$$

and

$$C = \frac{|N_2 - N_1|}{N_1 + N_2},$$

where $N_1$ and $N_2$ are the total number of items (brood plus adults) observed within nests 1 and 2, respectively. $P_{N1}$ is the proportion of colony in nest 1, and $C$ the overall cohesiveness of the colony, ranging from 0 (equal split between both nests) to 1 (unanimous choice of a single nest). Colony distribution was preferred over absolute nest choice as a measure of nest preference because of the high occurrence of splitting (27 out of 70 colonies in experiment 1). The numbers of adults and brood items within nests were highly correlated (Pearson’s correlation, all colonies: $r = 0.99, t = 90.15, \text{d.f.} = 215, p < 5 \times 10^{-16}$; split colonies only: $r = 0.85, t = 127.21, \text{d.f.} = 60, p < 5 \times 10^{-16}$).

Using the combined distribution of brood and adults to measure nest preference and cohesiveness thus provided a global, unbiased representation of each colony’s decision.

In both experiments, all colonies experienced all treatments in a pseudo-random order (e.g. if there were two treatments, half the colonies first experienced treatment 1, then treatment 2; whereas the other half first experienced treatment 2, then treatment 1). Successive emigrations were separated by at least one week to minimize the effects of previous experience [34].

(d) Statistical analyses

Statistical analyses were performed using R v. 2.10.1 and MINITAB 15.1.

![Figure 2. Experiment 2. (a) (i) Diagram of the experimental set-up (Y1 and Y2: sister half-colonies from mother colony Y; ON, old nest, good, destroyed after the exploration week; FN, familiar nest, mediocre, visited by informed half-colonies during exploration; UN, unfamiliar nest, mediocre, never visited prior to emigration). (ii) Nest preference after 24 h (Wilcoxon matched-pairs test between treatments: $p = 0.37$). Squares, rectangles and whiskers, respectively, represent the median, interquartile range and full range of the proportion of colony items observed in the FN (dotted) or the UN (white). For each treatment, the data presented for the FN are complementary to the data presented for the UN (i.e. proportion in FN = 1 – proportion in UN). The dashed line represents expectations under the hypothesis of random choice between nests ($p$-values of corresponding median tests are given for each treatment). (b) Median number of ants in the FN (grey circles) and the UN (black squares) for informed (full symbols and lines) and naive (empty symbols and dashed lines) half-colonies as a function of time during the first hour of emigration. Analysis of covariance, n.s.: $p > 0.5$; ***$p < 0.001$.](http://rspb.royalsocietypublishing.org/lookup/doi/28128133108)
Colony distribution after 24 h was compared among treatments using Friedman tests for three related samples or Wilcoxon matched-pairs tests. Within treatments, colony distribution was compared to random expectations using median tests ($p = 0.5$).

In both experiments, discovery times of either the familiar or the unfamiliar nest did not differ across treatments (Mann–Whitney U-tests: $p > 0.4$ in all comparisons) and were therefore pooled for subsequent analyses. Discovery times of familiar and unfamiliar sites were then compared for each experiment using Wilcoxon matched-pairs tests.

In experiment 1, the frequency of splitting 24 h after emigration was compared across treatments using a generalized linear model (GLZ) with binomial data (split versus unanimous choice) implemented in R package MASS (function glm), followed by Tukey’s post-hoc tests. Cohesiveness was compared across treatments using a Kruskal–Wallis test, followed by Siegel and Castellan’s post-hoc tests [35].

In experiment 2, the median number of ants inside candidate sites during the first hour of emigration was analysed using a general linear model with time as a covariate, treatment (control or transfer), nest (familiar or unfamiliar) as fixed factors, and their interactions. Normality of residuals was checked using a Kolmogorov–Smirnov test (d.f. = 48, KS = 0.1, $p > 0.150$).

### 3. Results

(a) Experiment 1: the relative roles of positional cues and nest-marking chemicals on aversion

Nest preference differed strongly between the summer and winter replicates: in summer, control colonies showed a significant preference for the unfamiliar nest, whereas in winter, they showed a significant preference for the familiar nest (figure 1b,c; median tests: summer, $N = 23$, $p < 0.05$; winter, $N = 24$, $p < 0.01$). This indicates that in summer, colonies deemed the familiar, bright nest unsuitable and developed an aversion to it, whereas in winter they deemed it suitable and later emigrated to it preferentially.

In summer, colonies in the treatment exchange also significantly preferred the unfamiliar nest over the familiar nest, even though their position had been switched (figure 1b; median test: $N = 23$, $p < 0.05$). By contrast, in the treatment removal, colonies chose randomly between both unfamiliar nests, even though one was at the position previously occupied by the familiar nest (figure 1b; median test: $N = 24$, $p = 0.27$). Accordingly, nest preference differed significantly across treatments when considering the position of the new nests (figure 1b; Friedman test, $\chi^2 = 8.03$, d.f. = 2, $p < 0.05$), suggesting that positional cues play a negligible role in collective aversion.

By contrast, in treatments control and exchange—where colonies had a choice between a familiar and an unfamiliar nest—nest preference was consistent across treatments when considering the origin of the new nests (i.e. whether they had previously been visited or not; figure 1b; Wilcoxon matched-pairs test, $N = 22$, $Z = -0.421$, $p = 0.67$). This strongly suggests that the familiar nest had been marked chemically during the familiarization period, and that nest-marking chemicals played a major role in the collective rejection of that nest.

In winter, the opposite trend was observed: nest preference was consistent across treatments when considering the position of new nest sites (figure 1c; Friedman test, $\chi^2 = 4.07$, d.f. = 2, $p = 0.13$), whereas in treatments control and exchange, nest preference differed significantly when considering the origin of new nest sites (figure 1c; Wilcoxon matched-pairs test, $N = 23$, $Z = -2.248$, $p = 0.025$). This suggests that positional cues played a prominent role in collective nest choice in winter. Colonies overall tended to prefer the nest occupying the previous position of the familiar nest, but this was not significant in the absence of chemical cues (removal, median test: $N = 24$, $p = 0.31$) or when chemical cues were in conflict with positional cues (exchange, median test: $N = 23$, $p = 0.40$). This indicates that chemical cues—although not necessarily the same as the ones underlying collective aversion—also played a minor role in nest choice in the winter replicate.

Colony preference for unfamiliar over familiar nests in summer did not stem from differences in the time necessary for the ants to first find and enter these nests (figure 3; Wilcoxon matched-pairs test: $Z = -0.078$, $N = 12$, $p = 0.94$).

In summer, colonies in the treatment removal split significantly more often than in the other treatments (removal: 17 out of 24 colonies split; exchange: eight out of 23; control: two out of 23; GLZ, effect of treatment: $p < 0.00005$, Tukey’s post-hoc tests: R. versus C.: $p < 0.00005$; R. versus E.: $p < 0.05$; C. versus E.: $p = 0.10$). An overall measure of cohesiveness confirmed that colonies were significantly less cohesive in the treatment removal (figure 1d; Kruskal–Wallis test, $\chi^2 = 21.41$, d.f. = 2, $p < 0.00005$; Siegel–Castellan post-hoc tests: R. versus C.: $p < 0.00005$; R. versus E.: $p = 0.01$; C. versus E.: $p = 0.32$). By contrast, in the winter replicate there were no differences in splitting rate (removal: 12 out of 24 colonies split; exchange: nine out of 24; control: eight out of 24; GLZ, effect of treatment: $p = 0.48$) or in cohesiveness (figure 1e; Kruskal–Wallis test, $\chi^2 = 3.53$, d.f. = 2, $p = 0.17$) across treatments.

Overall, these results highlight strong seasonal differences both in collective nest preference and in the corresponding underlying decision-making mechanisms: in summer, colonies developed an aversion towards familiar, bright nests and nest choice was chiefly determined by the presence of a scent mark which (i) downgraded the perceived value of the familiar nest irrespective of its position and (ii) contributed to the maintenance of colony cohesion. In winter, by contrast, colonies showed an attraction towards familiar (albeit bright) nests, and nest choice was mostly influenced by positional cues. No effect of treatment on colony cohesion was detected in winter.
(b) Experiment 2: do nest-marking chemicals influence naive nest-mates?

Nest preference did not differ between informed and naive colonies (figure 2a; Wilcoxon matched-pairs test, \( N = 38, Z = -0.900, p = 0.37 \)). In both treatments, colonies significantly preferred the unfamiliar over the familiar nest (figure 2a; median tests; control: \( N = 38, p < 0.01 \); transfer: \( N = 38, p < 0.05 \)), indicating that they had developed an aversion to the familiar, bright nest upon exploration.

There was no difference in the discovery times of the familiar and unfamiliar nest sites in both treatments (figure 3; Wilcoxon matched-pairs test: \( Z = -0.360, N = 27, p = 0.72 \)). Additionally, during the first hour of emigration, the number of ants inside candidate sites increased over time in a similar way for the control and for the transfer treatment (figure 2b; covariance analysis; effect of time: \( F_{1,42} = 591.64, p < 0.001 \); effect of treatment: \( F_{1,42} = 0.02, p = 0.89 \); interaction nest \( \times \) treatment: \( F_{1,42} = 0.46, p = 0.5 \)). More specifically, the initially similar populations in both nests increased more quickly in the unfamiliar than in the familiar nest site for both treatments (figure 2b; covariance analysis, interaction nest \( \times \) time: \( F_{1,42} = 108.55, p < 0.001 \); effect of nest: \( F_{1,42} = 2.32, p = 0.135 \)).

These results show that the nest-marking chemicals laid by informed workers inside familiar nests triggered collective aversion towards those nests in naive sister colonies, even though workers in naive colonies had not previously been in contact with those nests. The nest-marking chemicals therefore provide social information about nest quality and influence collective nest choice; in doing so, they act as a modulatory pheromone that diminishes the probability of choosing a marked nest.

4. Discussion

In this study, we aimed to investigate the mechanisms underlying collective aversion towards low-quality, familiar nest sites in the ant T. albipennis. Surprisingly, we found that aversion was strongly season-dependent: colonies collected and tested in summer and in autumn developed an aversion towards bright nest sites, as reported in previous studies [24,26], whereas colonies collected and tested in January showed an attraction towards these sites. In agreement with a previous study, this indicates that bright nests are considered of low quality in summer and in autumn, whereas they are considered suitable after overwintering [31].

In agreement with a previous study [30], we found that preferential emigration towards the familiar nest in winter was predominantly influenced by positional cues, while chemical cues only played a secondary role. By contrast, collective aversion towards the familiar nest in summer depended crucially on the presence of nest-marking chemicals, while positional cues played a negligible role (if any). Although Temnothorax ants occasionally lay individual-specific chemicals [27–29], this was not the case here: naive colonies were able to decipher the message contained in nest-marking chemicals and showed as strong an aversion to the familiar nest as informed colonies. This indicates that the nest-marking chemicals underlying collective aversion are involved in intraspecific communication; hence they qualify as a pheromone [36,37]. The chemical nature of the aversive pheromone—as well as that of the chemical cues involved in post-overwintering attraction for familiar bright nests—are currently unknown.

The use of negative pheromones has already been reported in social insects: honeybee and bumble-bee foragers, for example, mark recently visited, exhausted flowers with chemicals that repel other foragers until nectar has been replenished [38,39]. A repellent pheromone has also been described in the Pharaoh’s ant Monomorium pharaonis, acting as a ‘no entry’ signal near trail bifurcations, which deters workers from entering non-rewarding trails [40]. Contrary to these examples, the aversive pheromone described here does not act as a repellent ‘no entry’ signal near the nest entrance. If that were the case, it would indeed decrease the rate of workers entering marked nests. This would result in both delayed first entrance and slower initial population increase in the marked versus unmarked nests—neither of which was observed. Rather, the aversive pheromone must label the interior of unsuitable nests and modulate subsequent nest evaluation by exploring workers, e.g. by downgrading the perceived value of marked nests. This in turns influences nest choice by the entire colony. Our results thus illustrate a novel mode of action of a negative pheromone, and indicate that the condition of independent evaluation was not satisfied in our experimental system.

Another type of negative signal has recently been described in honeybees: bees produce vibrational ‘stop signals’ providing negative feedback that reduces recruitment to perilous food sources [41] or helps reach consensus in nest-site selection [18]. During nest-site selection, scouts that have committed to a site use the stop signal to stop nest-mates from advertising concurrent sites through waggle dancing. Stop signals thus provide cross-inhibition between candidate sites and facilitate consensus formation. Notably, the stop signal affects recruitment and opinion pooling, but has not been shown to influence nest evaluation by individual bees. By contrast, the aversive pheromone appears to modify collective nest preference by influencing nest evaluation by individual ants. In agreement with theory [8], this violation of independent evaluation has been shown occasionally to decrease collective accuracy: recent work revealed that when the novel, unfamiliar alternative nest is of lower quality than the familiar mediocre nest, collective aversion towards the familiar nest significantly increases error rates in emigrating colonies [26].

Overall, our results thus suggest that—in agreement with recent claims—ants do not necessarily always aim to maximize their accuracy when selecting a new nest site [16,18]. In T. albipennis, colonies spontaneously move to better nest sites [42], so inaccurate choices can be easily corrected. Other aspects of the decision-making—such as the value of the chosen option, the time required to make a decision and the ability to reach consensus—may thus well be prioritized over accuracy [10,16,18,43]. In our experimental system, the use of the aversive pheromone may simply result from communication constraints: whereas the presence of a worker can be interpreted as a ‘vote’ in favour of a nest [15–17,30], the absence of a worker cannot be directly interpreted as a negative ‘vote’ against a nest—hence transferring information about the low quality of a site requires an indirect communication channel, such as chemical signalling. In addition, we found colonies to be more cohesive in the presence than in the absence of the aversive pheromone (summer replicate). At certain times of year, preserving colony cohesion in emigrations could be as important, or indeed more important, than choosing the best site. An interesting parallel can be drawn here with honeybee decision-making. A bee swarm needs to reach a consensus before it can fly to a unanimously chosen nest site [15]. The
stop signal plays a crucial role in avoiding deadlocks (i.e. inability to reach consensus) between sites of equal value by introducing cross-inhibition between populations of scouts committed to competing sites [18]. The inability to reach consensus would result in a lengthy decision-making process, as bee swarms do not split. In ants, the inability to reach consensus additionally favours splitting. The aversive pheromone therefore seems to play a role akin to that of the stop signal, by helping ant colonies to reach consensus (and thus remain cohesive) when choosing between otherwise equal sites. In that sense, lack of independent evaluation might be beneficial rather than detrimental.

The potential importance of cohesion in determining decision-making strategies in *T. albipennis* can be highlighted by considering its life cycle. *T. albipennis* (previously known as *Leptothorax tuberoininterruptus*, *L. tuberum* and *L. albipennis*) is seasonally polydomous: colonies split into several nests in early spring then coalesce in summer and overwinter in a single nest [22,23]. In spring, as late instar larvae develop into adult-size pupae, nest size can be a critical limiting factor for colonies producing large sexual brood. Indeed, colonies of the related species *Temnothorax curvispinosus* were shown to have lower brood populations after eight weeks in a small nest than colonies housed in larger nests [44]. Splitting in spring thus allows colonies to avoid nest overcrowding [45] and to forage more efficiently to feed developing brood [21]. By contrast, after the mating flight in early summer, space and food demands decrease and colonies reunite into a single nest [22,23]—e.g. to achieve better defence or more efficient thermoregulation via clustering [21,23]. Our results reveal a novel proximate mechanism that could contribute to the seasonal cycle of splitting and merging in *T. albipennis*. We found that colonies show seasonal fluctuations between aversion and attraction to bright nests. After overwintering, increased attraction to bright nests should lead to (i) a higher number of nest sites being simultaneously deemed suitable by a colony and (ii) less frequent use of the aversive pheromone, both of which favour splitting. By contrast, aversion to bright nests in summer and autumn could be useful in preparing for the cold season, because (i) it enhances cohesion, thus favouring colony merging before winter and (ii) it allows colonies to avoid overwintering in nests that are poorly isolated from adverse exterior conditions, as can be assessed based on within-nest light levels [31]. Season-specific aversion towards bright nests could thus complement other season-specific factors (such as annual variation in intranidal density [22]) that are likely to influence splitting rates [45,46].

It remains unclear which cues and stimuli are directly responsible for the seasonal expression of aversion versus attraction to bright nests. In our experiments, colonies were exposed to natural lighting, but temperature, humidity and pressure were not controlled to match external conditions. In addition, winter colonies had more brood than summer colonies (probably owing to the recent hatching of pupae in summer), and summer colonies had experienced a drastic reduction in number of reproductive individuals just before collection (during the mating flight). Lighting conditions, nest density (and in particular brood density), presence versus absence of reproductive individuals and the development of the brood are factors that are known to vary seasonally in the ant’s life cycle and may well trigger seasonal changes in the perceived attractiveness of bright nests—in the field and in our experiments. Alternatively (but not exclusively), seasonality could be tightly linked to an endogeneous circannual rhythm. The incidence of these factors in the seasonality observed here remains to be tested.

We showed that a previously unknown modulatory aversive pheromone, used to label low-quality nests, plays a fundamental role in the emigration process of *T. albipennis*. Although the mechanistic bases of seasonal behavioural changes have long been studied in vertebrates and some invertebrates (e.g. [47–49]), there have been few studies of the mechanisms underpinning seasonal changes in collective behaviour in eusocial insects beyond studies of social homeostasis [50,51]. Our study suggests new mechanisms for the seasonal ecology of nest-site selection in ants: seasonal variations in the perceived attractiveness of bright nests, leading to season-specific use of the aversive pheromone, are likely to help colonies modulate their decision-making strategy as ecological conditions vary. In addition, our results suggest that a strategy that appears detrimental when compared with other model systems (here, violation of independent evaluation) may be very successful in other contexts (here, propagation of information and increased cohesion). This highlights the importance of understanding optimality criteria [16,18] and avoiding generalizations when studying collective decision-making. Indeed, it is often impractical to prevent communication and enforce independence in humans [17], who are fundamentally social. Future studies on decision-making by teams and committees could focus on designing strategies taking advantage of communication among group members to improve collective decisions overall.

Acknowledgements. The authors would like to thank E. Franklin for her help in the field, T. O. Richardson for critical reading of the manuscript, and L. Keller, A. Le Boeuf, E. Lucas and C. Mullon for their input.

Data accessibility. All data are available from Dryad (doi:10.5061/dryad.2v4hv).

Funding statement. N.S. acknowledges PRES ‘Université de Toulouse’ and the ‘programme Lavoisier ‘Cotutelle de thèse’ du Ministère des Affaires étrangères et Européennes’ for funding. M.G. acknowledges the support of the CNRS, the University Paul Sabatier and the Institut Universitaire de France. N.R.F. acknowledges EPSRC grant EP/D076226/1 and BBSRC grant BB/C02166X/1.

References

19. Pirrone A, Stafford T, Marshall JAR. In review. When
33. Dehaut G, Schatz B, Elias M, McKey D. 2007 Polydomy in ants: what we know, what we think we know, and what remains to be done.
49. Bradshaw WE, Holzapfel CM. 2010 Light, time, and the physiology of biorhythms to rapid climate change in animals. Annu. Rev. Physiol. 72, 147 – 166. (doi:10.1146/annurev-physiol-021909-135837)