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Author for correspondence:
T. M. Schaerf
e-mail: timothy.schaerf@sydney.edu.au

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Do small swarms have an advantage when house hunting? The effect of swarm size on nest-site selection by *Apis mellifera*

T. M. Schaerf[1,2], J. C. Makinson[1], M. R. Myerscough[2] and M. Beekman[1]

[1]Behaviour and Genetics of Social Insects Laboratory, School of Biological Sciences, and Centre for Mathematical Biology, and [2]School of Mathematics and Statistics, University of Sydney, Sydney, New South Wales 2006, Australia

Reproductive swarms of honeybees are faced with the problem of finding a good site to establish a new colony. We examined the potential effects of swarm size on the quality of nest-site choice through a combination of modelling and field experiments. We used an individual-based model to examine the effects of swarm size on decision accuracy under the assumption that the number of bees actively involved in the decision-making process (scouts) is an increasing function of swarm size. We found that the ability of a swarm to choose the best of two nest sites decreases as swarm size increases when there is some time-lag between discovering the sites, consistent with Janson & Beekman (Janson & Beekman 2007 *Proceedings of European Conference on Complex Systems*, pp. 204–211.). However, when simulated swarms were faced with a realistic problem of choosing between many nest sites discoverable at all times, larger swarms were more accurate in their decisions than smaller swarms owing to their ability to discover nest sites more rapidly. Our experimental fieldwork showed that large swarms invest a larger number of scouts into the decision-making process than smaller swarms. Preliminary analysis of waggle dances from experimental swarms also suggested that large swarms could indeed discover and advertise nest sites at a faster rate than small swarms.

1. Introduction

One of the most appealing facets of collective behaviour is the ability of a group to succeed in situations where an individual would fail. The animal kingdom is replete with examples of cooperation such as in the gathering of resources [1–3], decision-making [4], house hunting [5–7], nest construction [8,9] and group movement [10].

Being a member of a large group is often advantageous for individual group members. For species under constant threat of predation, individuals can reduce the probability that they will be killed when they are in a large group because it becomes far more likely that another group member will be taken instead. Similarly, the likelihood of early detection of a predator through distributed vigilance increases with group size [11]. However, there are some collective processes that could suffer as a result of large group size. One such process is nest-site selection by the honeybee *Apis mellifera*. Nest-site selection is a complex but fairly well-understood process whereby a swarm of honeybees selects a new nest site after reproductive swarming [12]. The population of each colony divides and approximately three-quarters of the workers along with a colony's current queen leave their home and form a hanging cluster nearby (referred to as a *swarm* throughout this paper) [13]. The swarm's workers then must find a suitable location to establish a new home in a reasonable length of time. It is advantageous for swarms to pick the best possible site to found a new colony as otherwise the colony will be forced to move again. A simulation study [14] using the detailed, fine time-scale, agent-based model developed in Janson *et al.* [15] predicted that large swarms of *A. mellifera* could be prone to making suboptimal decisions in terms of the quality of the chosen nest site, whereas smaller swarms would make slower, but more accurate decisions. By contrast, recent experimental studies have shown a positive effect for larger swarms on the growth and survival of new colonies [13], and foraging performance when paired with the honeybees' unique dance communication [16]. Here, we further examine the effect that group size has on the nest-site selection process of *A. mellifera* through a combination of mathematical models and field experiments.

During nest-site selection, a small percentage of bees in the swarm (approx. 5% [17]), the scouts, fly out from the swarm in search of a new home, usually a cavity in a tree. When a scout finds a potential nest site, she spends some time assessing its quality. If the scout determines that the site is suitable, she returns to the swarm, and communicates the location of the site via a waggle dance [18,19]. The dance is composed of two distinct phases: a waggle phase, where a dancer walks forward in a straight line while waggling her abdomen vigorously, and a return phase, where the dancer follows a semicircular arc to the left or right back to her starting position before embarking on another waggle phase. Directional information is contained in the angle of the waggle phase and distance information is encoded in its duration [20]. The quality of a nest site is also encoded in the dance; dancers for good quality sites tend to produce more waggle runs on their return to the swarm than dancers for poor quality nest sites. Other bees crowd around the dancer, following it. Some of the dance followers may attempt to visit the site danced for, and if they find the site, will spend some time assessing it before returning to the swarm and attempting to recruit more bees via their own waggle dances. After a bee completes a waggle dance, she will return to the nest site and reassess its quality. She will then return to the swarm and dance again. The process of assessing a site and then returning to the swarm to produce another waggle dance can be performed multiple times. The number of dance circuits produced on each return to a swarm reduces linearly on average (dances decay at an average rate of 17.2 circuits per return, [21]) until ultimately a bee gives up on dancing for a site completely. This cessation of dancing for a nest site prevents sites from being advertised indefinitely. The approximately constant rate of dance circuit decay also guarantees that signals for good quality sites will persist for longer than signals for poorer quality sites, because the number of circuits produced on the first return to the swarm is a function of site quality.

Scouts devoted to particular nest sites engage in inhibitory stop-signalling while on the swarm [22]. A stop signal is applied to a dancing bee by another bee head-butting her in the side at the same time as producing a notable buzzing sound. If sufficient signals are applied to a dancer, then she may give up her current bout of dancing altogether. Stop signals seem to be applied most frequently to dances for a site different to the preferred site of the stop signaller (*contra* signals). Stop signalling has implications for decision speed and accuracy, reducing decision speed but improving decision accuracy, and is an important component in preventing deadlocks in decision-making [22].

Once the number of bees visiting a particular nest site at the same time reaches 10–40 bees, a *quorum* is reached [23]. The site at which the quorum is met is effectively chosen by the swarm as its new home. Bees that experience the quorum return to the swarm and attempt to rouse the rest of the swarm to prepare for flight by producing high-pitched, auditory, *piping* signals and jostling their way across the swarm performing vigorous *buzz* runs. Over time the tightly clustered swarm loosens and eventually takes flight; bees that know the location of the new nest site guide the rest of the swarm to their new home by a process of streaking (flying at high speed through the swarm in the direction of the new nest site) [24–27].

It is generally believed that the scouts involved in nest-site selection are likely to be older workers with previous foraging experience. The scouts would thus be drawn from a fraction of the mother colony. It follows that the number of scouts is proportional to swarm size. If the number of scouts is a function of swarm size, but the size of the quorum is fixed and independent of swarm size, then it is possible that decision accuracy decreases as swarm size increases. Qualitatively, if a scout from a large swarm discovers a mediocre nest site early in the decision-making process, she can recruit from a large pool of bees. The larger pool of available scouts means that bees are more likely to be recruited to examine the nest site than if fewer scouts were available. The number of bees visiting the site will then quickly reach the quorum, ending the decision-making process. Therefore, the problem for a large swarm might be that it will hastily choose a mediocre nest site before any independent scouts have the opportunity to discover a better one [14].

We sought to determine whether swarm size can influence decision quality through theoretical investigations and complementary experimental work. In our theoretical work, we used an established agent-based model [28,29] to examine whether swarm size could affect decision accuracy in problems of choosing between two nest sites (following the work of Janson & Beekman [14]) or more realistic problems of choosing between tens of nest sites. Our concurrent experimental work was used to test some of our model assumptions and predictions. In particular, we tested if the number of scouts involved in nest-site selection is an increasing function of swarm size (a fundamental assumption of our modelling) and if swarms of different sizes find and advertise nest sites at different rates. We also sought information on the number of nest sites that swarms discovered and advertised with waggle dances during nest-site selection.

2. Simulations—the possible effects of scout numbers on decision accuracy

Simulations performed by Janson & Beekman [14] suggest that swarms that have 300 or more scouts actively involved in the decision-making process could suffer a loss in decision accuracy compared with swarms that make use of fewer scouts. This loss in accuracy occurred in simulations where swarms were faced with a choice between two nest sites—a mediocre site discovered by the swarm at the beginning of the decision-making process, and a better quality nest site discovered at a user prescribed time of 4–6 h later. The quorum was fixed at 20 bees for all simulations, irrespective of swarm size [14].

Given that a suboptimal decision made by a swarm could have negative consequences for both the survival and reproductive output of the new colony, we decided to further study the role played by the number of scouts involved in decision-making using another established model. Our chosen model was the agent-based model of Passino & Seeley [28] that captures many of the details of the individual interactions involved in nest-site selection with the exception of inhibitory stop-signalling. Our goals in using the model were twofold: first to determine whether the trends in the reduction of decision accuracy observed by Janson & Beekman [14] were reproducible by an equivalent, but not identical, model over a wide range of swarm sizes and time-lags in site discovery; and, second, to examine the effect of scout numbers on decision accuracy for more realistic problems of choosing between many sites distributed over a large spatial range. We provide complete details of the model in the electronic supplementary material, S2 along with a flowchart showing the connections between individual states; a complete description of the model can also be found in Passino & Seeley [28,29]. We did not include inhibitory stop signalling in our model, and we assumed that the quorum required for a decision was fixed and independent of swarm size. Our rationale behind these modelling choices is provided in the electronic supplementary material, S2.

The model of Passino & Seeley [28] was originally used to study nest-site selection by swarms that made use of 100 scouts without any explicit reference to the total number of bees in a swarm. Most of the model can be used to study swarms of different sizes using the same parameter values examined in [28] without alteration. However, we reinterpreted the calculation of the probability that individual bees will scout independently so that it was a function of swarm size. Our underlying assumption was that the probability of encountering a single dance on the swarm diminishes as the size of a swarm increases. There is some experimental evidence to suggest that dances could be evenly distributed across the surface of a swarm during the later stages of nest-site selection [30], consistent with our assumption. Our assumption affected the way we selected the individual exploration parameter, σ. Additionally, we reformulated the equation that determines the probability of independent exploration, p_e, so that the effect of swarm size is explicitly included. The details of selecting an appropriate value for σ as a function of both swarm size and the number of available nest sites are provided in the electronic supplementary material, S3–S5.

One of the reasons we chose the agent-based model of Passino & Seeley [28] is that it explicitly models exploration by scouts searching for viable nest sites. The spatial domain that explorers travel over is modelled as a square grid with equally spaced discrete grid points in two spatial dimensions (x and y). Each grid point is assigned a value, $f(x,y)$, between 0 and 1 that represents the quality of the nest site at that point. Nest sites are usually limited to covering a small portion of the spatial domain, with most values of $f(x,y) = 0$. Explorer bees fly to a random point on the grid, whereas bees recruited by a waggle dance fly to the site corresponding to the dance that they observed. Both explorers and recruits then independently assess the quality of the site that they are attending. The assessment of a grid point's quality by bee j at time k is a function of its underlying value, $f(x,y)$, and a small amount of noise, $w^j(k)$, which is a uniformly distributed random variable on $[-0.1,0.1]$. Formally, bee j's assessment of the grid point at (x,y) is given by

$$S^j(k) = \begin{cases} f(x,y) + w^j(k) & \text{if } f(x,y) + w^j(k) > \varepsilon_t \\ 0 & \text{if } f(x,y) + w^j(k) \le \varepsilon_t \end{cases}, \qquad (2.1)$$

where ε_t is a predefined minimum threshold for an acceptable site. Bees with $S^j(k) > 0$ will become committed to the site that they visit, whereas those with $S^j(k) = 0$ will remain uncommitted and return to the swarm to observe and follow dances. On her first return to the swarm after finding an acceptable site, a scout will produce 150 $S^j(k)$ waggle runs (the best simulated sites will produce approx. 150 waggle runs, similar to experimental observations [28,31]); for each subsequent turn that she remains committed to that site she reduces the number of waggle runs in her dance by a constant 15 circuits (close to the observed rate of dance decay [21]). The explicit locations of nest sites are randomized at the start of each simulation.

For our first study, we used the model of Passino & Seeley [28] to examine decision accuracy of swarms of various size when faced with the problem of choosing between two nest sites: a mediocre nest site (site 1: $f(x_1, y_1) = 0.67$) and an outstanding nest site (site 2: $f(x_2, y_2) = 1.0$). Each swarm was placed at the centre of a grid of 21 × 21 grid points; grid points were interpreted as being separated by a distance of 300 m, so that the entire grid covered an area of 6 km × 6 km (following [28]). The probability of an individual discovering one of the suitable nest sites during an exploratory flight was therefore $1/(21 \times 21) = 1/441$ per site. The mediocre nest site was immediately discoverable by scouts, whereas the outstanding nest site was not discoverable until time t_1 (measured in minutes) of a simulation ($f(x_2, y_2) = 0$ until time t_1). At time t_1, a scout in the resting state (or the active state if there were no resting scouts) was randomly selected as the initial discoverer of site 2 by changing the scout's state to committed. Simultaneously, at time t_1, site 2 was made discoverable by all other bees by setting $f(x_2, y_2) = 1.0$. Simulations were run for a maximum of 64 time steps representing 30 min intervals (32 h in total) or until the quorum was reached.

We performed our calculations in two stages. For each swarm size, we determined the value of the exploration parameter σ that minimized $T_{\text{split}} + T_{\text{non}}$ (the sum of split and non-decisions); determination of these optimal values of σ was performed with zero time-lag in site discoveries ($t_1 = 0$). Simulations in the first stage (with $t_1 = 0$) were performed across a range of scouts numbers ($N \in \{50, 100, 150, \ldots, 1000\}$) and values of σ ($\sigma \in \{0.1, 0.2, 0.3, \ldots, 10.0\}$). We performed 100 simulations for each pair of N and σ; we then identified the value, or values, of σ for which $T_{\text{split}} + T_{\text{non}}$ was the lowest for each value of N. We then determined the median of all the values of σ that minimized $T_{\text{split}} + T_{\text{non}}$ across all swarm sizes. We used this median value ($\sigma = 2.0$) for subsequent simulations involving a choice between two nest sites.

For each swarm size N, we then performed 1000 simulations for times $t_1 \in \{30, 60, \ldots, 360\}$ (with $\sigma = 2.0$ for all N). For each swarm size and t_1, we counted the number of times site 1 and site 2 were selected. For swarms that made use of 500 scouts or more, we found that there was a visible decrease in decision accuracy as swarm size increased (characterized by a decrease in the number of times the best nest site, site 2, was chosen, and an increase in the number of times that site 1 was chosen, see figure 1). The decrease

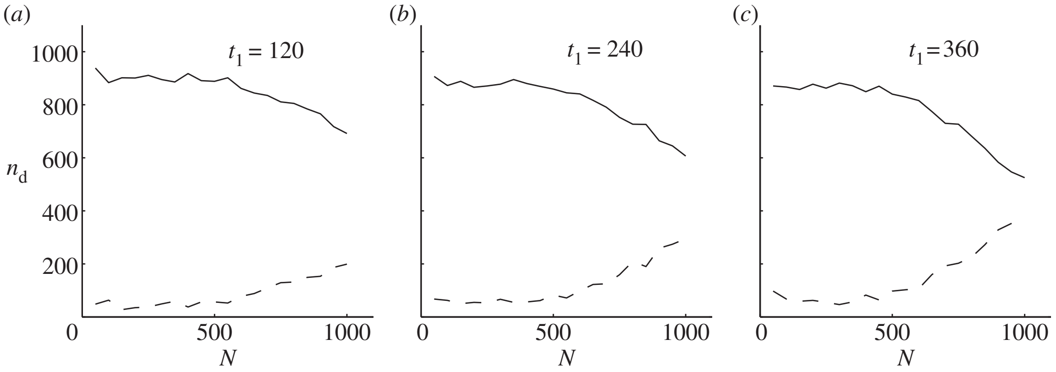

Figure 1. The number of decisions made, n_d, for selected time lags, t_l, for the first discovered, mediocre nest site (site 1—dashed line) and the excellent quality nest site (site 2—solid line) as a function of the number of scouts involved in the decision-making process, N. Panels are plotted in ascending order of t_l from (*a–c*).

in decision accuracy became more marked as swarm size increased and was also present for swarms that made use of fewer than 500 scouts. These results complement those found by Janson & Beekman [14] and indicate that swarms that make use of a large number of scouts could be less accurate in their decisions than small swarms.

The standard problem examined in most modelling studies of the bees' decision-making process [15,22,28,29,32–38] and in some controlled experimental studies (e.g. [6]) is to give swarms a choice between two to six nest sites (but see [39] for a modelling study with a choice between 120 distinct nest sites). Natural honeybee swarms are likely to be faced with a greater number of potential nest sites to choose between. To construct what we believed was a relatively realistic nest-site selection problem for our simulated swarms, we randomly placed 30 nest sites of varying quality throughout a large spatial domain.

Each simulated swarm was placed at the centre of a grid of 61 × 61 points so that the entire grid covered an area of 18 km × 18 km. Simulations were again run for a maximum of 64 time steps of half an hour duration. We performed two sets of simulations: one set for a swarm that used a relatively small number of scouts and one set for a swarm that used a relatively large number of scouts. We used the mean rates at which our real experimental swarms produced new dancers as the basis for the number of scouts available to our simulated swarms (see §3). For small swarms, the mean rate at which new dancers appeared was $\bar{r}_t = 10.98$ dancers per hour; thus over the 32 h of our simulations, small swarms had $N = 10.98 \times 32 \approx 351$ scouts in total. Similarly, our experimental large swarms produced new dancers at a mean rate of $\bar{r}_t = 27.30$ dancers per hour, and our simulated large swarms had a total of $N = 27.30 \times 32 \approx 873$ scouts in total. Thirty nest sites were randomly distributed over the spatial grid for each simulation. The quality of these nest sites was given by $f(x, y) = \{0.1, 0.125, 0.15, 0.175, \ldots, 0.8, 1.0\}$. The problem of choosing between these sites is complicated because there are many sites to choose from, the quality difference between the sites is small in most cases (0.025 except for the difference in quality between the best nest site and the second best nest site) and the probability of discovering any of the individual sites is low (1/3721 per explorer on a grid of 61 × 61 = 3721 points). All sites were discoverable from the beginning of each simulation.

For both small and large swarms, we first determined the value of the parameter σ that minimized $T_{\text{split}} + T_{\text{non}}$ within the 32 h time limit. For each swarm size, we performed 1000 simulations for each $\sigma \in \{0.1, 0.2, 0.3, \ldots, 10\}$. For our simulated small swarms, $\sigma = 1.7$ minimized $T_{\text{split}} + T_{\text{non}}$; for our simulated large swarms, $\sigma = 1.9$ minimized $T_{\text{split}} + T_{\text{non}}$. The median of the two optimal values of σ was then used for comparisons across swarm size. We ran an additional two sets of 1000 simulations each (one set with $N = 351$, the other set with $N = 873$ and $\sigma = 1.8$ for both sets of simulations). From these simulations, we determined the accuracy of the decisions made by the optimal swarms. Small swarms chose the best nest site 469 times, and large swarms chose the best site 597 times (figure 2*a*). Small swarms made 779 decisions (out of 1000) for a single site within the time limit; when the best site was not chosen small swarms chose one of the alternative sites 310 times. Small swarms formed split decisions 173 times and failed to make a decision 48 times. Large swarms made 843 decisions within the time limit; 246 of these decisions were for a site other than the best. Large swarms formed 145 split decisions and failed to make a decision 12 times. Coupled with the greater decision accuracy for large swarms was a faster decision speed (figure 2*b*). Distributions of decision times were different for small and large swarms ($p = 1.17 \times 10^{-5}$, two-sample Kolmogorov–Smirnov test). Small swarms made successful decisions in a mean duration of 14.43 h (standard deviation: 5.77 h). Large swarms made successful decisions in a mean time of 13.25 h (standard deviation: 4.55 h).

Contrary to the predictions made by our earlier simulations using two nest sites only, large swarms were more accurate than small swarms at solving the more realistic problem that we set for them. We believe the primary reason for the difference in accuracy for small and large swarms simulated with the agent-based model is connected to the enhanced exploratory capability of large swarms. A large swarm will be able to explore the landscape more rapidly than a small swarm owing to its greater number of scouts. As a consequence, many of the potential nest sites will be found earlier in the decision-making process and with a sufficiently small time lag until the best site is found. Thus, errors associated with rapid recruitment are mostly avoided. Figure 3 illustrates that our large simulated swarms discovered nest sites at a faster rate than small swarms (where site discovery is determined by the time that the first dance for a particular site was produced; $t = 0$ for the first time step of simulation).

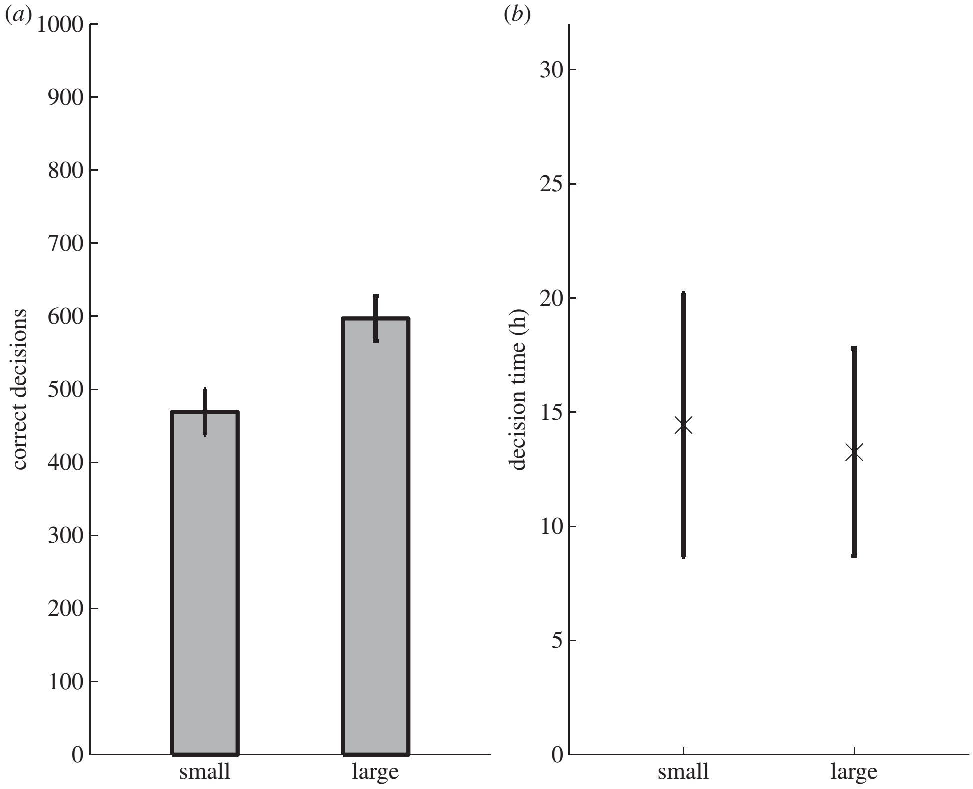

Figure 2. The effect of swarm size on (*a*) decision quality and (*b*) decision time for simulations that gave swarms a choice between 30 different nest sites. (*a*) The total number of times that the best-quality nest site was chosen throughout 1000 simulations for both small and large swarms. In Error bars represent the upper and lower limits of the 95% binomial proportion confidence interval estimated using Matlab's intrinsic *statbinoci* function (with success corresponding to selection of the best site within the time limit, and failure corresponding to any other outcome). (*b*) Error bars are plotted one *standard deviation* above and below the mean time that a decision was made for either the small or large simulated swarms.

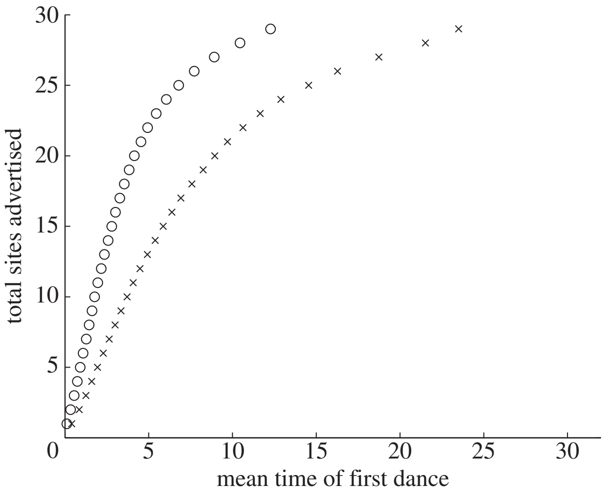

Figure 3. The total number of unique nest sites advertised on the swarm (throughout the entire decision-making process) as a function of time (in hours) for small simulated swarms (cross symbols) and large simulated swarms (circles). Dances for different nest sites need not take place simultaneously.

3. Swarm experiments

3.1. Material and methods

Swarm experiments were performed between 28 September 2009 and 20 January 2010 at the University of Sydney's Cromelin Field Station, Pearl Beach, New South Wales, Australia (latitude: 33.55° S, longitude: 151.30° E). We prepared eight small swarms composed of approximately 5000 bees, and eight large swarms composed of approximately 15 000 bees using the standard procedure described in Beekman *et al.* [25]. Complete details of swarm preparation and field observations are provided in the electronic supplementary material, S8.

For each day, i, of each swarm's activity, we calculated the total length of time (to the nearest minute) that the swarm was actively involved in decision-making, t^i_{daily}. t^i_{daily} was measured from the time of the first observed dance each day until the time of the last observed dance for the same day. When rain inhibited the activity of the swarm (on 10–11 October 2009 for one small swarm, and 13 November 2009 for another small swarm), we subtracted the total duration of the rain periods from t^i_{daily}. We also removed any data on the limited dance activity during periods of rain from our dataset. The total duration of a decision-making process across m days was then defined as $t_{\text{total}} = \sum_{i=1}^{m} t^i_{\text{daily}}$. We estimated the rate at which new dancers appeared on swarms each day, i, via $r_{\text{d}} = n^i_{\text{d}}/t^i_{\text{daily}}$ and the rate at which new dancers appeared on the swarms throughout the entire decision-making process via $r_t = n_t/t_{\text{total}}$, where n^i_{d} is the number of unique dancers observed during day i and $n_t = \sum_{i=1}^{m} n^i_{\text{d}}$.

From video data, we analysed waggle dances that occurred during the entire decision-making process of one small swarm (labelled swarm S7), the first day of decision-making of the second small swarm (labelled swarm S8; approx. 8 h of data) and the entire decision-making process of the large swarm (swarm B8; approx. 6 h of data). To assist in our analysis, we developed a Matlab program that determines the bearing and duration of individual waggle runs based on user input (this approach was inspired by the method used by Klein *et al.* [40] to analyse waggle dances). The main component of our program worked by placing a transparent Matlab figure over an external video player window (SMPlayer). Video was played back at slow speed (usually at 1/4 speed); using mouse input, the program's user would click on a dancing bee's thorax once at the beginning of a waggle run and once again at the end of a waggle run. The angle of each dance circuit relative to vertically upwards was determined using coordinates recorded at each mouse click; the duration of each circuit was determined by the duration between consecutive pairs of mouse clicks and the video playback speed. Ultimately, we determined the direction indicated by each waggle run with the assistance of data on the azimuthal position of the sun (http://www.susdesign.com/sunposition/index.php). The distance to a location indicated by a dance circuit was estimated from dance durations using a dance calibration formula obtained for *A. mellifera mellifera* by Beekman *et al.* [41]. Finally, we determined the mean dance location indicated by each dance from the locations indicated by each component waggle run. We did not record all waggle runs that occurred on the surface of the swarm; instead, we recorded all waggle runs that occurred on the swarm during 30 s intervals, with the start of each interval separated by a period of 5 min (measured from the start time of our video footage). From swarm S7, we analysed a total 247 waggle runs from 30 dances, from swarm S8, we analysed 2473 waggle runs from 271 dances and from swarm B8, we analysed 2704 waggle runs from 474 dances.

We estimated the number of different sites indicated by our set of mean dance locations using an algorithm originally developed to estimate the number of forage patches advertised by colonies of *A. mellifera* [41] (see the electronic supplementary material, S9, for an outline of the method). The algorithm takes into account the variability in waggle dance information as a function of the distance to advertised sites. We determined the time that each nest site was first advertised on the respective swarms. We performed linear regression analysis on each of these datasets and hence estimated the rate at which swarms advertised new nest sites (from the slope of each regression line).

3.2. Results

Large swarms produced new dancers at a greater rate than small swarms based on both r_t and r_d. We performed several calculations to verify this result. Based on categorical data, r_t is significantly different for large swarms versus small swarms ($p = 0.0497$, two-sample Kolmogorov–Smirnov test of data from eight small and eight large swarms). Large swarms issued new dancers at a mean rate of $\bar{r}_t = 27.30$ dancers per hour (and a standard deviation of 15.11 dancers per hour); small swarms had $\bar{r}_t = 10.98$ dancers per hour with a standard deviation of 6.94 dancers per hour. There was a significant linear relationship between swarm size, n_b, and r_t (line of best fit: $r_t = 0.0015n_b + 3.4598$, Pearson correlation coefficient $r = 0.56$, $F_{1,14} = 6.45$, $p = 0.02$), and a significant linear relationship between swarm size and r_d (line of best fit: $r_d = 0.0015n_b + 4.1577$, Pearson correlation coefficient $r = 0.59$, $F_{1,20} = 10.88$, $p \approx 0$).

There was no significant difference in the length of time it took large swarms to make a decision versus the time it took small swarms to make a decision ($p = 0.79$, Kruskall–Wallis one-way ANOVA). For large swarms, the mean time to make a decision $\bar{t}_{\mathrm{total}} = 8.01\,\mathrm{h}$ with a sample standard deviation of 4.78 h. For small swarms, $\bar{t}_{\mathrm{total}} = 8.06\,\mathrm{h}$ with a sample standard deviation of 4.56 h.

During the periods of video data analysed, we found that swarm S7 advertised 10 nest sites, swarm S8 advertised 22 nest sites and swarm B8 advertised 30 nest sites. Figure 4 illustrates the number of unique sites that each swarm danced for as a function of time. Swarm S7 advertised new nest sites at an approximate rate of 3.57 sites per hour ($r = 0.98$, $F_{1,8} = 202.41$, $p = 5.80 \times 10^{-7}$), swarm S8 advertised new nest sites at an approximate rate of 2.42 sites per hour ($r = 0.98$, $F_{1,20} = 594.60$, $p = 2.38 \times 10^{-16}$) and swarm B8 advertised new nest sites at an approximate rate of 5.91 sites per hour ($r = 0.96$, $F_{1,28} = 308.42$, $p = 1.19 \times 10^{-16}$). Owing to the limited sample size (two small and one large swarm), we cannot say anything definitive about the rate at which small and large swarms produce dances for new nest sites. However, the above analysis does not contradict model-based predictions that large swarms discover nest sites at a faster rate than small swarms.

4. Discussion

Our initial modelling work supported Janson & Beekman's [14] idea that swarms that make use of relatively large numbers of scouts are prone to making suboptimal decisions, especially when there is a significant time lag between the discovery of nest sites. In reality, swarms could be faced with a choice between many potential nest sites, so it could be artificial to enforce a large time lag in site discovery to ensure that the best site is always discovered late in the decision-making process. Our more realistic simulations, incorporating a large number of potential nest sites that were readily discoverable, suggest that swarms that have a large number of scouts have an advantage over swarms that use a smaller number of scouts in choosing one of the best available sites. Instead of a large number of scouts being a disadvantage, because a decision is reached too quickly, our results show that a large group of scouts is able to more rapidly survey the surrounding landscape and find suitable nest sites than a smaller group of scouts. Analysis of a subset of our large and small experimental swarms supports the notion that large swarms are better able to explore their environment. These theoretical and experimental results are consistent with the apparent ability of large colonies to find and recruit to resources more quickly during foraging than smaller counterparts [16]. Our experimental work further confirms that large swarms indeed make use of more scouts than their smaller counterparts. Thus, scouts are most probably drawn from a fraction of the total population of a swarm.

Given that we did find an effect of swarm size on decision accuracy under some conditions, and on the swarm's ability to discover and choose a good nest site when many sites are available, can a swarm be either too small or too large? Natural swarms of *A. mellifera* can range from just over 2400 to 41 000 bees, with a mean size of approximately 11 800 bees [42]. There appears to be no correlation between the size of swarms and the volume of cavities that swarms settle in [43,44]. Thus, it seems likely that swarms of all sizes seek cavities within the same range of volumes and have the same range of nest sites to choose from. We have some

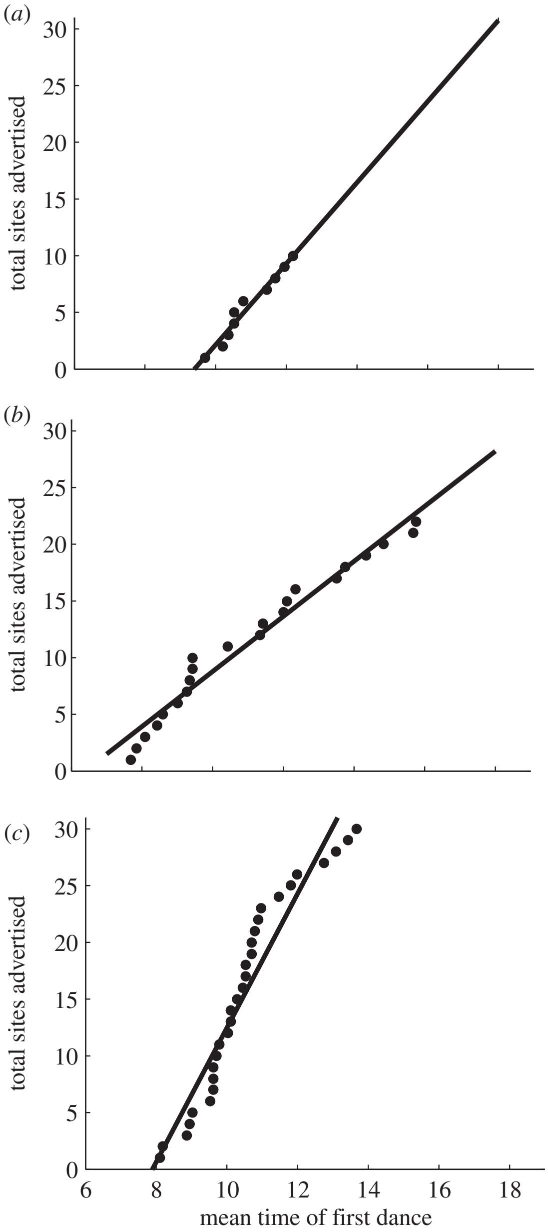

Figure 4. Estimated total unique nest sites advertised via waggle dances as a function of time for experimental swarms. Individual plots are for (*a*) small swarm S7, (*b*) small swarm S8 during the first day of decision-making and (*c*) large swarm B8. The large swarm B8 produced dances for new nest sites at a greater rate than either swarm S7 or swarm S8.

experimental evidence that small *Apis* swarms have trouble making a decision. Makinson *et al*. [45] performed a series of nest-site selection experiments with artificial swarms of the red dwarf honeybee, *Apis florea*. This species has colonies that are much smaller than those of *A. mellifera* and therefore also has much smaller swarms. One of the artificial swarms prepared by Makinson *et al*. [45] was composed of approximately 1600 bees and only produced seven unique dancers, both relatively small numbers even for *A. florea*. The swarm struggled to make a decision over a period of 6 days; during the third day, it seemed to be preparing for flight but was unsuccessful in leaving. The decision-making process of *A. florea* resembles that of *A. mellifera*, although the process differs in some details [39,45–47]. Importantly, *A. florea* seems to conclude its decision-making process based on a sufficient number of dancers agreeing on an approximate location to travel to, analogous to the quorum used by *A. mellifera* [45]. It therefore seems that a problem faced by very small *A. mellifera* swarms could be an inability to recruit sufficient bees to a particular nest site to pass the quorum threshold.

By contrast, a very large swarm will have a huge pool of scouts at its disposal. Qualitatively, one possible drawback for a large swarm might be that several nest sites of similar quality are found early in the decision-making process. It would then be possible for the quorum to be reached for multiple sites at similar times, resulting in a split decision. Split decisions are extremely rare in experimental conditions, but they have been observed (e.g. [19]). To explore the possibility of swarms being too large further, we performed additional simulations using the model of Passino & Seeley [28] similar to those in the electronic supplementary material where swarms were presented with a simpler problem of choosing between six nest sites on a smaller grid (see the electronic supplementary material, S3), but with a swarm that made use of 2000 scouts. We found that a swarm with a very large number of scouts is indeed susceptible to split decisions; the way this manifests in the model is that it is not possible to pick an appropriate value of the exploration parameter, σ, that reduces the percentage of split decisions below approximately 20%. Simulated swarms with up to 1000 scouts always had a percentage of split decisions below 2.5% when faced with the same choice between six nest sites (see the electronic supplementary material, S3; figure 2*e*).

Our relatively small and large simulated swarms (that made use of 351 and 873 scouts, respectively) do not reflect the extremely small and large swarm sizes that might be incapable of making any sort of decision or are prone to split decisions as outlined above. However, some of the trends from our simulations were consistent with our expectations with regard to small and large swarms. Small swarms were less capable of making a decision within the given time limit, and when they did make a successful decision, it took longer than it did for our large swarms. Contrary to our prediction above, small swarms were also more predisposed to making split decisions than the large swarms (17.3% of simulations for small swarms resulted in a split decision compared with 14.5% of simulations for large swarms). The relatively large proportion of split decisions seen in both our large and small swarms is a result of our selection criteria for σ, which favoured the ability to make any sort of decision over failing to make a decision within the time limit.

In general, our results are consistent with the idea that the speed and accuracy (measured in terms of selecting the best available nest site within range of a swarm) of nest-site choices is strongly influenced by a swarm's ability to gather information about the surrounding environment, which in turn is a function of swarm size. Based on our experimental result that showed similar decision times for small and large swarms, it seems that larger honeybee swarms could sacrifice some of their potential numbers-based decision speed in favour of making a better decision, but not so much that they take longer to make a decision than small swarms.

Nest-site selection by honeybees shares fundamental characteristics with other natural systems that exhibit speed-accuracy trade-offs in decision-making [7,36,48]. Such systems are often modelled in the context of making a choice between two alternatives (see [49] for a review). The shared components of these models are that evidence favouring each alternative is integrated over time (for honeybees this is the process of discovering and evaluating nest sites), the accumulation process is subject to noise (for honeybees some of the components of this noise include the random nature of site discovery and inaccuracies in communicating site quality and location via waggle dances) and the decision's conclusion is based on the accumulation of sufficient evidence favouring one alternative over others (for honeybees this is achieved via a *quorum*). The beauty of the bees is that we can actually manipulate the system to further investigate the underlying mechanisms that govern decision-making in decentralized biological systems.

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