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The effect of individual learning on collective foraging in honey bees in differently structured landscapes

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The trade-off between exploiting known resources and exploring for new ones is a complex decision-making challenge, particularly when resource patches are variable in quality and heterogeneously distributed in the landscape. Social insect colonies navigate this challenge, in the absence of centralized control, by allocating different individuals to exploration or exploitation based on variation in individual behaviour. To investigate how heritable differences in individual learning affect a colony's collective ability to locate and choose among different quality food resources, we develop an agent-based model and test its predictions empirically using two genetic lines of honey bees (*Apis mellifera*), selected for differences in their learning behaviour. We show that colonies containing individuals that are better at learning to ignore unrewarding stimuli are worse at collectively choosing the highest-quality resource. This work highlights how differences in individual behaviour may have unexpected consequences for the emergence of collective behaviour.

Fitness strongly depends on an animal's ability to find resources. However, animals often face trade-offs between exploiting known resource patches and exploring for new ones. How animals resolve this trade-off is influenced by the characteristics of the environment, such as how resources are distributed spatially in the landscape (Anderson, 2001; Hart, 1981; Hewitson, Dumont, & Gordon, 2005; Stephens & Krebs, 1986) and the variability of resource quality (Charnov, 1976; Kohlmann & Risenhoover, 1998; McNamara, 1982). If most resource patches are similar in quality, organisms should persist in known patches, as long as those patches remain sufficiently profitable (Charnov, 1976) because exploration is unlikely to yield something better. However, if resource patches are highly variable in quality, it is beneficial to invest in exploring the environment to increase the chances of finding and exploiting the most rewarding resources.

How an individual balances time between exploration and exploitation can be influenced by how they learn. Within species, there are often differences among individuals in learning characteristics, including learning speed (Chittka, Dyer, Bock, & Dornhaus, 2003; Couvillon, Degrandi-Hoffman, & Gronenberg, 2010), accuracy (Chittka et al., 2003) and the ability to reverse learned associations (Chandra, Hosler, & Smith, 2000). Because of cognitive constraints, individuals often covary in these learning abilities, such that 'fast' learners are good at quickly focusing in on relevant stimuli, at the cost of being less accurate or flexible in their decision making, while 'slow' learners make decisions more accurately and with greater flexibility (Bitterman, Menzel, Fietz, & Schafer, 1983; Mazza, Eccard, Zaccaroni, Jacob, & Dammhahn, 2018; Sih & Del Giudice, 2012; Tait & Naug, 2020).

This variation among individuals may be maintained partly because different learning styles are beneficial in different environments. When resources differ in quality, organisms must decide when to accept patches they find and when to continue searching for better ones. Individuals that learn faster and ignore irrelevant information may be better at quickly exploiting resources (Chittka, Skorupski, & Raine, 2009; Sih & Del Giudice, 2012) and therefore perform better when all patches are similar. On the other hand, individuals that learn slowly and incorporate new information more readily may spend more time exploring and therefore be

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better at choosing the best available resources when patches differ substantially in quality (Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015; Guillette, Reddon, Hoeschele, & Sturdy, 2011; Katsnelson, Motro, Feldman, & Lotem, 2011; Sih & Del Giudice, 2012). These differences among individuals in decision-making strategy may also be related to other elements of personality, such as the bold—shy continuum, in addition to differences in learning ability (Sih, Bell, & Johnson, 2004).

Animals living in social groups have the unique ability to engage in exploration and exploitation simultaneously by allocating each of these tasks to different individuals. In eusocial insects with irreversible queen and worker castes, the colony tends to be the unit of selection (Seeley, 1997). Differences in learning among workers in a colony can enhance the colony's foraging success, because different individuals can specialize in either locating resources or exploiting them. In a honey bee colony, a small fraction of foragers act as scouts, who specialize in searching for new food resources, while the rest of the foragers exploit these resources (Biesmeijer & de Vries, 2001; Seeley, 1983). Scouts share information about the location (Dyer, 2002; von Frisch, 1967), odour (Farina, Grüater, & Díaz, 2005; Farina, Grüter, & Arenas, 2012) and quality (Jack-McCollough & Nieh, 2015; Seeley, Camazine, & Sneyd, 1991; Seeley, Mikheyev, & Pagano, 2000) of resources they discover using the waggle dance (von Frisch, 1967). The higher quality a discovered resource is, the longer and more vigorously a scout will recruit other foragers to it and the more likely it is that recruits will recruit others, generating positive feedback (Seeley et al., 2000). The colony's collective decision of which resource patches to exploit emerges from these quality-based differences in recruitment, without the need for individual foragers to sample or compare multiple patches (Camazine & Sneyd, 1991; de Vries & Biesmeijer, 1998; Seeley et al., 1991).

Just like solitary animals, a colony's investment in exploration and exploitation should depend on characteristics of the resource landscape. Previous theoretical work predicts that small resource patches, high patch density and low search costs should increase a social group's optimal investment in exploring (Johnson, Hubbell, & Feener, 1987). Other work suggests that the benefits of exploitation through social recruitment are highest when resources are difficult to find, patchily distributed and variable in quality (Donaldson-Matasci & Dornhaus, 2012; Dornhaus, Klugl, Oechslein, Puppe, & Chittka, 2006; Sherman & Visscher, 2002). Colonies that invest more in exploitation (e.g. via recruiting) should therefore perform better when resources are clumped in the landscape, i.e. are non-randomly grouped, while colonies that invest more in exploration (e.g. via scouting) should perform better when resource patches are evenly dispersed throughout the landscape. Furthermore, when resource patches differ in quality, colonies that invest more in exploitation should be better at choosing the highest-quality patch, while colonies that invest more in exploration should be better at finding patches quickly. Here we examined the way in which individual learning interacts with the spatial distribution of resources to influence a colony's foraging decisions at the collective level.

Variation among individuals in cognitive ability can influence the division of labour between workers that specialize in scouting for new resources and those that specialize in exploiting known resources. Although it is not fully understood what causes certain individuals to act as scouts (Beekman, Gilchrist, Duncan, & Sumpter, 2007; Dreller, 1998; Katz & Naug, 2015; Liang et al., 2012; Mattila & Seeley, 2007), there is evidence that variation in scouting tendency is linked to differences in learning, neurotransmitter levels and gene expression (Cook et al., 2018; Lemanski, Cook, Smith, & Pinter-Wollman, 2019; Liang et al., 2012). One learning behaviour that has been recently linked with scouting in honey bees is latent inhibition, the tendency to ignore stimuli that have been previously encountered without a reward (Chandra et al., 2000; Lubow, 1973). In the laboratory, individuals with high latent inhibition (LI) act like ‘fast’ learners, preferring novel to familiar stimuli and persisting in their learned associations, while individuals with low LI act like ‘slow’ learners, paying attention to both novel and familiar stimuli and easily reversing learned associations (Chandra et al., 2000; Cook et al., 2020; Tait & Naug, 2020). In the field, scout bees have been found to exhibit higher LI than recruit bees (Cook et al., 2018), suggesting that a ‘fast’ learning style is associated with exploration rather than exploitation in honey bee foragers. Ignoring previously unrewarding ‘familiar’ stimuli may help scouts seek new food resources quickly, while lower latent inhibition may allow recruits to continue exploiting depleting patches until new ones are located (Cook et al., 2018; Mosqueiro et al., 2017).

Individual differences in expression of latent inhibition are heritable in honey bees (Chandra et al., 2000; Chandra, Hunt, Cobey, & Smith, 2001; Cook et al., 2020), and there is natural variation in latent inhibition within a colony because of the genetic diversity that results from a queen mating with multiple drones. Latent inhibition is exhibited by drones and queens as well as by workers, making it possible to artificially select lineages of honey bees that are higher or lower than average in latent inhibition (Chandra et al., 2000; Cook et al., 2020). Workers from these artificially selected lines display similar latent inhibition to their parents, regardless of their adult social environment (Cook et al., 2020). The ability to genetically select bees for latent inhibition allows us to experimentally manipulate the composition of colonies to explore how individual learning affects colony level foraging behaviour in different environmental situations.

Here we examined how the latent inhibition (LI) of individual workers affects the collective foraging behaviour of honey bee colonies in differently structured landscapes. We predicted that the behavioural composition of colonies would influence the colony level allocation of workers to exploration (via scouting) and exploitation (via recruitment). We further predicted that when resource patches are variable in quality, the allocation of workers to exploration or exploitation would affect a colony's ability to find and exploit the highest-quality resource patch. Because scout bees tend to exhibit high LI (Cook et al., 2018), we predicted that colonies composed of high LI individuals would contain more scouts and, as a result, would be better at finding all available resource patches quickly. Because recruits tend to exhibit low LI, and collective decisions in honey bees emerge from differential recruitment (Seeley et al., 1991), we predicted that colonies composed of low LI individuals would be better at differentially exploiting the highest-quality resource patches. Furthermore, theory suggests that colonies that invest more in exploration should be better at finding evenly dispersed resources, while colonies that rely more on recruitment should be better at exploiting clumped resources (Dornhaus et al., 2006; Johnson et al., 1987). We therefore predicted that colonies composed of high LI individuals would collect more food when resources are evenly distributed in the environment while colonies composed of low LI individuals would collect more food when resources are clumped, i.e. concentrated in a few large patches.

To answer these questions, we first developed an agent-based model to explore the effects of environmental features on the foraging behaviour of honey bee colonies composed of a wide range of ratios of exploring and exploiting individuals (Fig. 1a). We then tested our model predictions empirically by placing honey bee colonies that were genetically selected for either high or low LI in environments that differed in the distribution of resources, which differed in their quality (Fig. 1b).

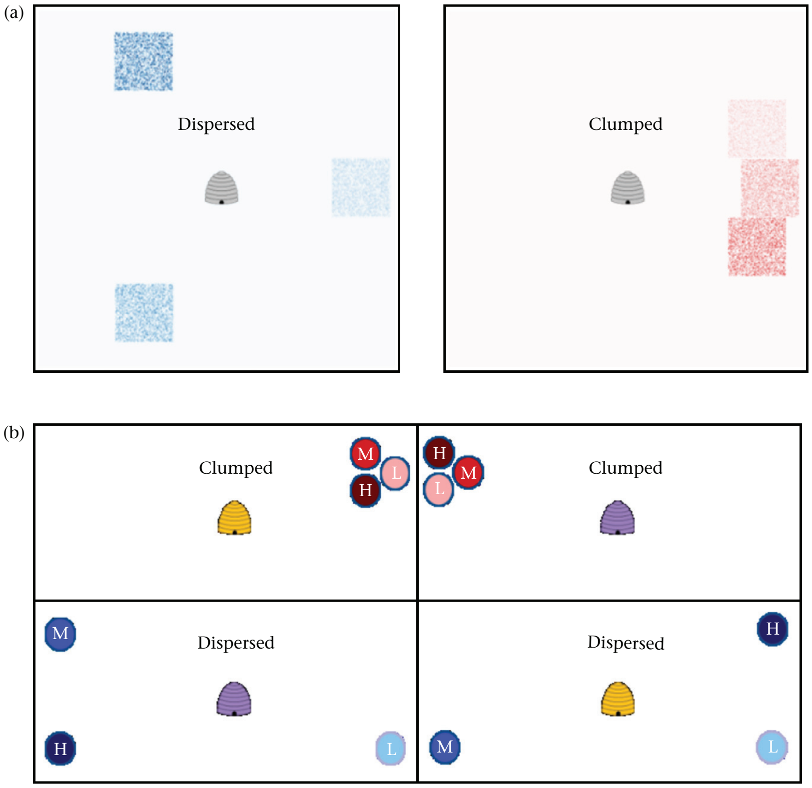

Figure 1. Spatial distribution of resource patches of different qualities in the (a) agent-based model and (b) empirical experiment. (a) Simulated resource landscapes in the agent-based model, with the symbol in the centre indicating the hive. Squares are resource patches, with darker hues indicating higher quality. (b) Experimental set-up of colonies in the empirical study. Each compartment (large rectangle) is a 30 × 108 m flight tent. Coloured symbols in the middle of each tent depict a bee hive. Hive colour indicates whether the colony is from a high (yellow) or low (purple) LI genetic line. Circles indicate feeders, with darker hues indicating higher quality and the letter inside indicating sucrose concentration (H: high (2.5 M), M: medium (1.5 M) and L: low (0.75 M)). Clumped treatment is in red and dispersed treatment in blue. After 2 days in this configuration, the experimental set-up was flipped such that the top two flight tents received dispersed feeders in the open corners of the tent and the bottom two tents received clumped feeders in the open corner of the tent.

METHODS

Agent-based Model

To examine how the distribution of food resources in the landscape influences the exploration–exploitation trade-off, we developed a spatially explicit agent-based simulation of colony foraging behaviour as a modification of a previous model by Mosqueiro et al. (2017). Full model details are presented in the Overview, Design concepts, and Details (ODD) format (Grimm et al., 2020) in the Supplementary Materials and may also be found on Github. For a full list of model parameters, see Table 1. The model was implemented using Python v.2.7.

To examine how colonies choose among different quality resources, we simulated a resource landscape, represented as a 36 × 36 m, two-dimensional grid, with the hive at the centre. The landscape had three 5.76 × 5.76 m nondepleting resource patches, each located 14.4 m from the hive. Each resource patch had a different quality q, defined as the amount of food bees collected in a single foraging load (Fig. 1a). The low-quality patch offered 1 resource unit per load, the medium-quality patch offered 2 units, and the high-quality patch offered 3 units. For bees, this is analogous to nectars with different sugar concentrations because load size is limited by the volume of a forager's crop, where it carries the nectar load (Wolf & Schmid-Hempel, 1989).

To uncover the effect of resource distribution on colony foraging, we simulated two different spatial distributions. In the ‘dispersed’ distribution, the three resource patches were evenly spaced in a circle around the hive (Fig. 1a). The resources were each 14.4 m from the hive and located 120° from each other, relative to the hive. In the ‘clumped’ distribution, all three resource patches were adjacent but not overlapping, with the centres of the patches 24° from each other relative to the hive (Fig. 1a).

Simulated colonies contained two types of foragers: scouts, which searched for food independently, and recruits, which waited to be recruited to food sources by nestmates. Forager flight dynamics were modelled as a biased random walk: at each time step, a forager's movement direction was the sum of its drift vector and a random angle drawn from a uniform distribution from $-\theta/2$ to $\theta/2$, where θ is the movement error parameter (Codling, Plank, & Benhamou, 2008; Mosqueiro et al., 2017; Reynolds, Smith, Reynolds, Carreck, & Osborne, 2007). At the beginning of the simulation ($t = 0$), all foragers started at the hive. At $t = 1$, scouts left the hive in a random direction and continued flying until they found food or reached the end of the foraging arena, at which point they returned directly to the hive.

Upon returning to the hive, successful scouts recruited inactive foragers (‘recruits’) with probability qw_s, where q is the quality of the located resource and the constant w_s is the scout baseline dancing probability (see Table 1 for parameter values). Scouts remained at the hive recruiting exploiters for 50 time steps, where each time step represents approximately 1.2 s. Scouts then returned to the located resource until their number of trips to that location was equal to their persistence parameter, π. After visiting a food patch π times, scouts left the hive in a new random direction to continue exploring. Recruits remained inactive in the hive until recruited to a resource by another forager. Once recruited, recruits left the hive in the advertised direction and flew until they found food, at which point they returned to the hive. On returning to the hive, recruits also recruited inactive exploiters with probability qw_r, where parameter w_r is the recruit baseline dancing probability (Table 1). Recruits then returned to the located resource until their number of trips to that location was equal to their persistence parameter, π at which point they became inactive at the hive until recruited again. We performed a sensitivity analysis to determine whether changing the value of π affected our results, and we did not find a qualitative effect of the value of π on our results (Appendix, Fig. A1). Each simulation ran for 21 000 time steps, which is equivalent to 7 h of simulated time, a typical foraging duration for bees (von Frisch, 1967).

To examine how the proportion of scouts in the colony and resource distribution jointly affected collective foraging, we varied the ratio of scouts from 10% to 90% of the foragers in the colony, in 10% intervals. For each scout proportion, we simulated both dispersed and clumped resource distributions. Colonies were always composed of 100 foragers. For each combination of scout ratio and resource distribution, we performed 150 simulation runs. To assess how the proportion of scouts and resource distribution jointly influence collective foraging, for each run, we calculated the number of visits foragers made to each feeder as well as total food collected by the colony at the end of the simulation. We also calculated net food collected, defined as total food collected minus total energy expended by foragers. We defined each forager's energy expenditure, dE, for each time step t, as:

$$\mathrm{dE}_t = a + b\,(\mathrm{dx}_t)^3$$

where dx is the distance that a forager travelled at time step t and a and b are constants based on the literature (Mosqueiro et al., 2017) (Table 1).

Finally, for each resource distribution, we calculated the optimal proportion of scouts as that which resulted in the highest net food collection.

Empirical Experiments

We performed all empirical work at Arizona State University's Honey Bee Research Lab on the Polytechnic campus in Mesa, Arizona, U.S.A.

Genetic Line Selection

To create genetic lines selected for high or low latent inhibition, we reared queens by grafting 1-day-old larvae into queen cups and placing them into a queenless colony with nurse bees (‘queenbank’). After emergence, we placed queens into cages and back into the queenbank for 7–10 days to mature. To obtain drones for the line selection procedure, we collected mature drones as they returned to a colony from mating flights in the late afternoon and isolated them in mesh cages inside the queenbank overnight. We tested both queens and drones for latent inhibition using the procedure described below, individually marked them using water-based acrylic paint pens (Montana Cans, https://www.montana-cans.com/en/marker-inks/acrylic-marker-ink/acrylic-markers/) and returned them to the queenbank to await insemination for no longer than 2 days.

Latent Inhibition Procedure

We scored the latent inhibition of queens and drones using a proboscis extension reflex (PER) conditioning protocol (Smith & Burden, 2014). We secured individuals in a plastic harness, so that they could only move their antennae and proboscis. To ensure that these bees responded to sucrose, which is essential for the PER protocol, we presented each bee with a drop of 1 M sucrose to the antennae and discarded any individual that did not extend its proboscis. We then fed each bee 7 μl of 1 M sucrose and allowed it to acclimate to the apparatus for 30 min. We familiarized bees to one of two odours (2-octanone or 1-hexanol), both readily learned by honey bees (Smith & Menzel, 1989), by presenting each bee with 40 unreinforced 4 s bursts of odour at 5 min intertrial intervals. To test the effect of familiarization on subsequent reinforced learning,

Table 1
Model parameters used in agent-based simulation

Parameter	Definition	Value(s)
c	Patch size	5.76 × 5.76 m
p	Patch density	0.6
d	Patch distance from hive	14.4 m
q	Patch quality (sugar concentration)	1 M, 2 M, 3 M
w_s	Scout baseline dancing probability	0.33
w_r	Recruit baseline dancing probability	0.1
γ	Recruitment rate	5/min
t_r	Time spent recruiting	1 min
v_s	Scout average flight speed	1
v_r	Recruit average flight speed	1.5
θ_s	Movement error while exploring for new patches	5
θ_r	Movement error while exploiting a known patch	2
a	Energy consumption intercept	1e-5
b	Energy consumption slope	1e-6
T	Total simulation time	7 h
n	Number of simulation runs	150
f	Number of foragers	100
s	Number of scouts	10–90
π	Number of times a forager returns to last visited patch	20

The simulations examined the effect of changing the number of scouts in the colony, the persistence of scouts and recruits, and the distribution of the three food patches. All other parameters were held constant in all simulations.

we allowed bees to rest for 30 min, then exposed them to either the familiar odour or to a novel odour, four times each, in a pseudorandom order. Both odours were equally reinforced as follows. We presented each odour for 4 s, and if the bee extended its proboscis in the first 3 s, we recorded it as a positive response. Upon extending its proboscis or after 3 s, we rewarded the bee with a 0.4 μl droplet of 1.5 M sucrose directly to its proboscis (Chandra, Wright, & Smith, 2010).

We calculated LI scores as (number of positive responses to the novel odour + 1)/(number of positive responses to the familiar odour + 1) and classified individuals with scores greater than 2 as high LI and individuals with scores less than 2 as low LI (Cook et al., 2020). We created high and low LI lineages by instrumentally inseminating high or low LI queens with like drones. We inseminated each queen with a single drone using standard instrumental insemination procedures (Cobey, Tarpy, & Woyke, 2013), then placed her into a nucleus colony of 5000 workers for approximately 1 month to build up a worker population. We then placed these colonies into standard nine-frame Langstroth hives and monitored them weekly to ensure no supersedure of the inseminated queen occurred. Previous work showed that workers from these high and low LI genetic lines exhibit similar LI to their parents (Cook et al., 2020).

Experimental Colony Creation

To create colonies of a single behavioural type for the experiment, we placed approximately 600 newly emerged workers from the colonies described above, marked by queen origin, of each LI type into experimental nucleus colonies. We created four experimental colonies of high LI workers and four colonies of low LI workers (eight colonies total), providing a sample size twice as large as previous work on colony level behaviour in honey bees (Nouvian et al., 2018). To supplement the worker population of these experimental colonies, we added approximately 600 control bees from nonselected colonies. To allow the high and low LI workers to reach foraging age, we waited 2 weeks before beginning the experiment.

Data Collection

To determine the foraging behaviour of the selected colonies in environments with different resource distributions, we allowed colonies to forage in a controlled environment. We collected data over a 2-week period, during 1–12 October 2018. We tested four colonies each week: two high LI and two low LI. Overnight, we placed each colony into the centre of a 30 × × 108 m mesh flight tent. Previous studies showed that bees engage in normal foraging behaviour in tents this size (Cook et al., 2020; Liang et al., 2012). We allowed colonies to acclimate to the tents for 1 day with access to water. Due to adverse weather on the first week of the experiment, we allowed colonies tested on that week to acclimate to the tents for 2 days. After acclimation, to induce foraging behaviour and to allow new foragers to become accustomed to artificial feeders, we provided colonies with artificial feeders containing 1 M sucrose solution scented with geraniol 2 m from the hive for 1 day.

To assess colonies' abilities to choose among different quality food sources, we placed three feeders of different quality in each tent on each day of the experiment. Each feeder contained 100 ml of sucrose solution. The high-quality feeder contained 2.5 M sucrose, the medium-quality feeder contained 1.5 M sucrose, and the low-quality feeder contained 0.75 M sucrose (Fig. 1b). For resources at this distance from the hive, foragers typically perform round dances, which, like waggle dances, have been shown to contain directional information (Waddington & Kirchner, 1992). In addition, dance followers can be recruited to particular resources using odour information (Farina et al., 2005, 2012; Grüter & Farina, 2009). To facilitate recruitment, we paired each quality feeder with a unique colour/odour combination. The odours used were 2-octanone, 1-hexanol and acetophenone. Previous experience suggests no innate difference in attractiveness of the odours used (Smith & Menzel, 1989). Still, to control for possible differences in attractiveness, we gave each set of high and low LI colonies a different quality colour–odour combination. Each colony experienced the same quality colour–odour combination throughout the course of the experiment.

To manipulate the distribution of resources, we tested two feeder configurations, clumped and dispersed. For two high LI and two low LI colonies, we placed the experimental feeders in a clumped configuration, with all three feeders closely spaced in a single corner of the flight tent (Fig. 1b). For the other two high and two low LI colonies, we placed the feeders in a dispersed configuration, with each feeder in a different corner of the flight tent (Fig. 1b). To avoid biasing foragers towards a particular direction, all feeders in the dispersed configuration were in different corners from the feeders in the clumped configuration (Fig. 1b). After 2 days, we switched the feeder distributions so that colonies that first received the clumped treatment received the distributed treatment and vice versa, and we collected data for 2 more days. To evaluate the colonies' foraging behaviour, we recorded the number of foragers that visited each feeder every 10 min for 7 h starting approximately at 0900 hours. We only counted foragers as visitors if they landed on the part of the feeders where food was accessible.

To measure the amount of food consumed, we weighed each feeder upon deployment and every 30 min throughout the experiment. We calculated daily food consumption as the difference between initial and final feeder weight each day. To determine whether evaporation had a different effect on the different sucrose concentrations, we placed three feeders containing 2.5, 1.5 and 0.75 M sucrose solution each in a separate mesh enclosure from which bees were excluded. These control feeders experienced similar temperature and light conditions as the experimental ones. We quantified evaporation from each control feeder as the difference between the weight when a feeder was deployed and its weight 7 h later.

Data Analysis

To determine how colony latent inhibition and resource distribution jointly influenced the colonies' visits to different quality feeders, we performed a generalized linear mixed model (GLMM) with total number of visits per day as the response variable with a Poisson log link function. We performed a second GLMM with daily food consumption as the response variable with a normal distribution and a log link function. In both models, we included colony latent inhibition, resource distribution and feeder quality as fixed effects. We included colony identity (ID) and date as random effects to account for variation among colonies and for weather conditions, respectively. We fitted both models by maximum likelihood using Laplace approximation and the BOBYQA optimizer. Visual inspection of the residuals revealed no deviation from normality. We performed all analyses in R v.3.5.2 (R Core Team, 2018), using the 'lme4' package (Bates, Mächler, Bolker, & Walker, 2015). To determine the confidence in our estimates, we performed a type II Wald chi-square test on the GLMM results, using the 'Anova' function in the R package 'car' (Fox & Weisberg, 2019).

To examine whether the three concentrations differed in evaporation rates, we performed a linear mixed model (LMM) with weight lost from the control feeders as the response variable, concentration as a fixed effect and date as a random effect.

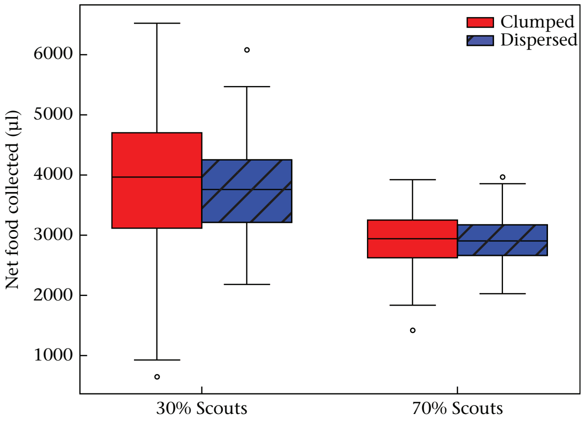

Figure 2. Effect of resource distribution on net amount of food collected in the agent-based model. Simulated colonies with low (30%) and high (70%) proportion of scouts when resources were clumped (red) or dispersed (blue). Net food was the total amount of food collected at the end of the simulation period, minus the energy expended by scouts and recruits during foraging. Here and in all following boxplots, horizontal lines are the medians, boxes and whiskers indicate first and second quartiles, and dots are outliers.

Ethical Note

This work was conducted in accordance with the ASAB/ABS Guidelines for the use of animals in research. Honeybees are invertebrates and so do not require special institutional permissions for experimentation. However, we took extreme care not to harm bees during preparation and experimentation. We handled and marked bees carefully, ensuring we did not damage their wings, we wore PPE and used smoke to avoid bee stings, because when bees sting, they die. Bees were placed back into the general apiary after the experiments ended. Colonies were kept indoors and in a quiet location until bees were 2 weeks old. We used naïve foragers to prevent flying bees from attempting to leave the flight cages, to decrease the likelihood of bee death from collisions with the tent. Bees were provided food and water ad libitum, and flight cages were equipped with water sprinklers to prevent overheating and ensure highest possible survival and welfare. All experiments took place on Arizona State University property and no endangered or protected species were involved in this study.

RESULTS

Agent-based Model

In our simulations, colonies with a low proportion of scouts collected 29% more food on average than colonies with a high proportion of scouts, but with 54% higher variance between model runs (Fig. 2). The proportion of scouts in a colony also affected the colony's ability to distinguish between resources of different qualities. Colonies with a lower proportion of scouts were better at choosing the highest-quality food source, visiting it 4.4 times more than the lowest-quality food source, compared to colonies with a high proportion of scouts, which visited the high-quality food source only 1.9 times more than the low-quality food source (Fig. 3). Thus, if high LI colonies contain more scouts, our model predicted that in the empirical experiment, the low LI colonies should be better than high LI colonies at differentially exploiting the highest-quality feeder.

Contrary to previous work (Dornhaus et al., 2006; Johnson et al., 1987), our model showed that the spatial distribution of resources only weakly influenced the optimal investment in scouting. This difference may be due to the fact that resources in our 'dispersed' condition were more heterogeneously distributed than in previous models. As a result, the difference in patch heterogeneity between the 'clumped' and 'dispersed' landscapes in our model may not have been large enough to affect the scouts' ability to locate all three resource patches. Regardless of the proportion of scouts, simulated colonies were better at differentially exploiting the highest-quality food source when resources were clumped than when resources were dispersed (Fig. 3). Furthermore, the optimal proportion of scouts was higher when resources were clumped (~40%) than when they were dispersed (~30%) (Fig. 4). Our model therefore predicted that both high and low LI colonies should choose higher-quality feeders, and collect more food, when the resources are clumped compared to when they are dispersed. A sensitivity analysis showed that changing the value of forager persistence, π, did not qualitatively change the model outcome (Appendix, Fig. A1). Higher persistence resulted in higher total food collection but did not affect the relationship between resource distribution and optimal scout number or patch choice.

Empirical Experiments

Colonies composed of high or low LI individuals differed significantly in their response to feeder quality (Fig. 5). Low LI colonies strongly preferred to visit and consume more food from higher-quality feeders over lower-quality feeders, regardless of feeder distribution (GLMM: colony LI × quality; visits: $\chi^2 = 292.01$, $P < 0.001$; consumption: $\chi^2 = 166654.01$, $P < 0.001$). In contrast, high LI colonies showed a weak preference for visiting higher-quality feeders when the feeders were clumped but not when the feeders were dispersed and they did not differ in their food consumption from different quality feeders in either resource distribution (GLMM: colony LI × feeder distribution × quality; visits: $\chi^2 = 17.37$, $P < 0.001$; consumption: $\chi^2 = 4928.69$, $P < 0.001$). Colonies from low LI lines also showed higher overall foraging activity than colonies from high LI lines, as evidenced by higher visit and food consumption rates (GLMM: colony LI; visits: $\chi^2 = 27.10$, $P < 0.001$; consumption: $\chi^2 = 180542.3$, $P < 0.001$).

Furthermore, high and low LI colonies differed significantly in how resource distribution affected foraging behaviour (Fig. 5). As predicted by our model, low LI colonies visited feeders more frequently and consumed more food when feeders were clumped compared to when they were dispersed. In contrast, high LI colonies visited feeders more frequently and consumed more food when feeders were dispersed compared to when they were clumped (GLMM: colony LI × feeder distribution; visits: $\chi^2 = 4.17$, $P = 0.041$; consumption: $\chi^2 = 7511.26$, $P < 0.001$). For full output of the statistical model see Appendix, Tables A1 and A2.

The weight lost due to evaporation in control feeders was very small (mean ± SD = 10.12 ± 6.22 g) relative to the amount removed by honey bees in the experimental feeders (27.89 ± 36.02 across all three concentrations). Still, higher sugar concentration had a significantly slower rate of evaporation in the control feeders (concentration: $\chi^2 = 4.62$, $P = 0.03$), as would be predicted by Raoult's law (Staverman & van Santen, 1941). Because the relationship between evaporation and sugar concentration was

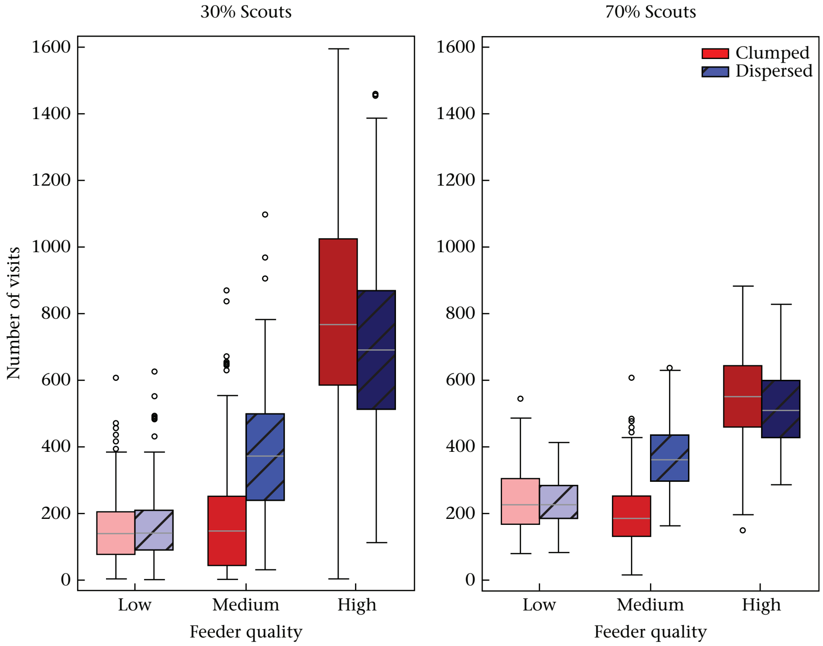

Figure 3. Visits to different quality food patches by simulated colonies with a low and high proportion of scouts. Colonies with a low (30%) or high proportion (70%) of scouts foraged on clumped (red) or dispersed (blue) resources that were of low (light hue), medium (medium hue) or high (dark hue) quality.

opposite to the relationship between concentration and food consumption observed in our experimental feeders, evaporation most likely caused us to underestimate empirical differences in forager consumption between the different concentrations.

DISCUSSION

Our results demonstrate that individual differences in learning affect collective decision making of groups in a different way than they affect decision making of solitary individuals. Our simulation predicted that colonies containing fewer scouts and more recruits would be better at choosing the best quality patches in a landscape in which resource patches differ in quality (Fig. 3). This simulation result emerged from the fact that scouts in the model were indiscriminate regarding which patches they exploited, while recruits in the model preferentially exploited higher-quality patches. Given that previous empirical work found that scouts tend to be high in LI (Cook et al., 2018), we predicted that more foragers would act as scouts in high LI colonies and that low LI colonies would be better than high LI colonies at focusing their foraging effort on higher-quality patches. Our empirical results confirmed this prediction (Fig. 5). Colonies composed of low LI bees, which are less exploratory as individuals, were better at choosing the highest-quality patches to exploit. Thus, our results demonstrate that in a social

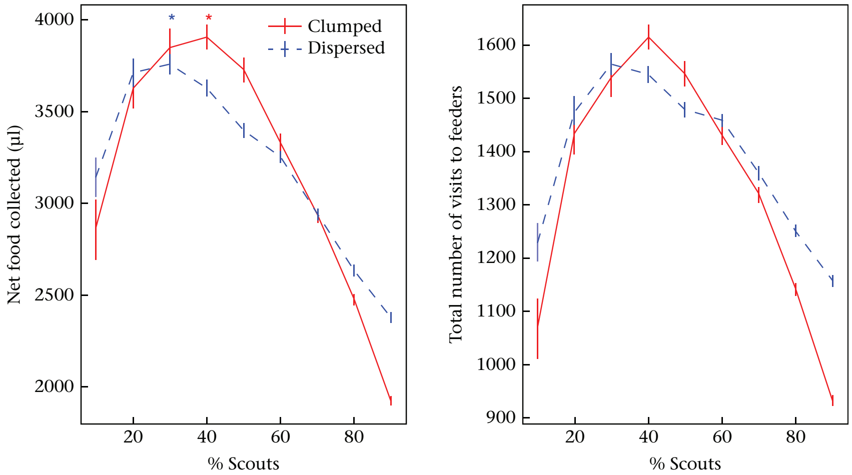

Figure 4. Effect of resource distribution on resource collection by simulated colonies with different proportions of scouts. Net food collected (left panel) was the amount of food collected at the end of the simulation minus energy expended from foraging on clumped resources (red solid line) or dispersed resources (blue dashed line). Total number of visits to feeder (right panel) is the number of visits to all three feeders. We simulated colonies with 10%–90% scouts in 10% intervals. Asterisks indicate the optimal proportion of scouts for each food distribution. Vertical lines are standard errors of 150 simulation runs.

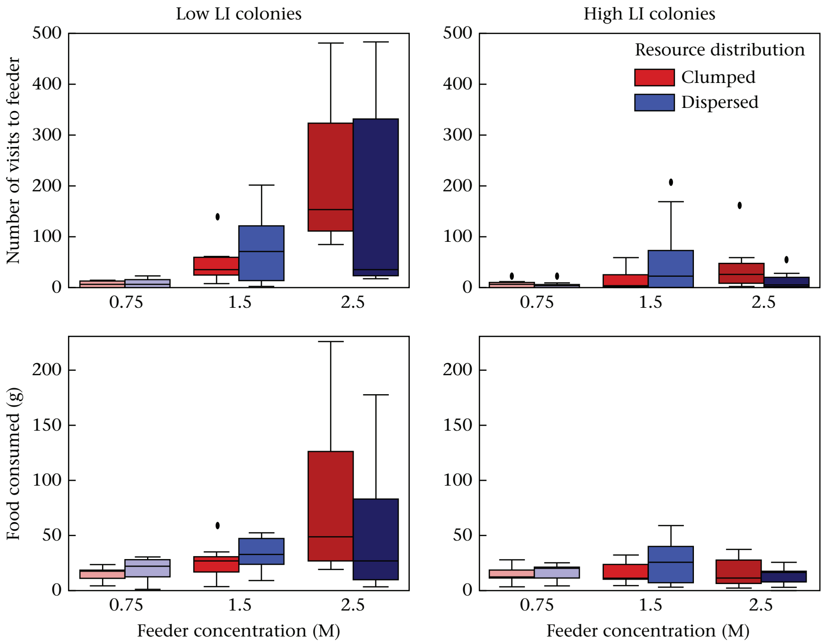

Figure 5. Foraging behaviour of experimental colonies from empirical work. Number of visits by foragers (top) and amount of food consumed (bottom) per day by colonies that were artificially selected for low (left) or high (right) latent inhibition (LI). Resources were clumped (red) or dispersed (blue) and differed in quality, with darker colours indicating higher sucrose concentration.

group, explorers help the group make decisions quickly while exploiters help the group make decisions accurately.

These results can be explained by the nature of collective decision making in honey bee colonies. Previous work has shown that each individual bee usually inspects only one available option and recruits other individuals to that option in proportion to the resource's quality (Dyer, 2002; Jack-McCollough & Nieh, 2015; Seeley et al., 1991). The colony's choice of which resource to exploit emerges from the differences in recruitment among patches, rather than any individual directly comparing options (de Vries & Biesmeijer, 1998, 2002; Seeley, 1995). High latent inhibition helps scouts to quickly find resources and report on their location and profitability to the group (Cook et al., 2020). Meanwhile, low latent inhibition helps the pool of recruits to sample broadly among advertised resources. Because dances for higher-quality resources attract more recruits, this broad sampling drives the majority of recruits to exploit the best patches. As long as a colony had sufficient scouts to locate high-quality patches, a larger number of exploiters resulted in greater utilization of the most rewarding patch by the colony as a whole.

These results highlight a key difference between the exploration–exploitation trade-off in social animals and in solitary animals. While we initially thought of high and low LI bees as explorers and exploiters, it may be more accurate to describe them as ‘finders’ and ‘refiners’: the high LI finders explore outside the nest for available resources to advertise and the low LI refiners collectively choose the best available option by differentially recruiting to advertised resources based on their quality (Cook et al., 2020). A colony needs enough searchers to locate available options, but the refiners are the ones who choose among them, so the colony can exploit the highest-quality patch. Indeed in the model, we see similar dynamics to the empirical experiments because the simulated scouts, like high LI foragers, are indiscriminate about what they exploit, but the simulated recruits, like low LI foragers, are discriminatory in what they exploit.

In addition to choosing the highest-quality food patch (Fig. 3), our model predicted that colonies with fewer scouts would collect more total food than colonies with more scouts (Fig. 2). In the model, this difference occurred because, once a few scouts located the high-quality patch, a large number of recruits could quickly exploit it without having to waste time searching for it independently. Similarly, in our empirical study, the low LI colonies collected more total food because, once a few foragers found the high-quality food source, they mounted a stronger recruitment response compared to the high LI colonies (Fig. 5). Because recruitment is the process by which the colony discriminates high-quality patches from low-quality ones, having a strong recruitment response increased both the total food collected and the differential utilization of the best patch.

Our simulation model predicted that the optimal investment in exploration should be higher when resources are clumped than when they are dispersed (Fig. 4). However, in contrast to this prediction, our empirical work showed that low LI colonies collected more food when resources were spatially clumped, while high LI colonies collected more food when resources were evenly dispersed resources (Fig. 5). Our finding that colonies with low LI bees performed better with clumped resources is consistent with previous theoretical and empirical work suggesting that the benefit of recruitment information in honey bees and other social insects is greatest when resources are clumped in large patches rather than evenly dispersed (Donaldson-Matasci & Dornhaus, 2012; Dornhaus et al., 2006; Johnson et al., 1987; Sherman & Visscher, 2002). Characterizing high and low LI individuals as finders and refiners, instead of explorers and exploiters, may further explain why the colonies of low LI bees collected more food in the clumped resource distribution while colonies of high LI bees collected more in the dispersed distribution. Previous experiments have shown that recruitment by the waggle dance is subject to error (Tanner & Visscher, 2010). When resources are clumped, individuals that are recruited to a known patch may accidentally discover nearby patches as well. In contrast, a broad search pattern such as a Lévy flight is most effective for finding randomly dispersed resources (Reynolds et al., 2007; Viswanathan et al., 1999).

Conclusions

Because resources are often patchily distributed and differ in quality, gathering information about the environment is a key component to foraging success. Our results suggest a novel solution to the exploration/exploitation trade-off in social groups through a division of labour between finders, who explore broadly for available resources, and refiners, who collectively choose among discovered resources to allow the group to focus its exploitation on the most rewarding patches. Our work suggests that finders and refiners differ in how they learn about resources, with finders learning associations quickly by focusing their attention on novel stimuli and refiners making decisions accurately by focusing their attention broadly on all available options. However, the collective response to the environment is not simply an additive property of individual learning, but an emergent property of the interactions among these different types of individuals.

Author Contributions

N.L. conducted the theoretical work, analysed the data and wrote the first draft of the manuscript. N.L. and N.P.W. designed the simulation and outlined the manuscript. N.L., N.P.W., C.N.C. and B.H.S. designed the empirical experiments. N.L. and C.N.C. carried out the empirical experiments. C.O. established and maintained the bee lines. All authors commented on the manuscript.

Declarations of Interest

None.

Acknowledgments

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References

Anderson, C. (2001). The adaptive value of inactive foragers and the scout–recruit system in honey bee (*Apis mellifera*) colonies. *Behavioral Ecology, 12*(1), 111–119. https://doi.org/10.1093/oxfordjournals.beheco.a000372

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 1*(1). Retrieved from https://www.jstatsoft.org/v067/i01.

Beekman, M., Gilchrist, A. L., Duncan, M., & Sumpter, D. J. T. (2007). What makes a honeybee scout? *Behavioral Ecology and Sociobiology, 61*(7), 985–995. https://doi.org/10.1007/s00265-006-0331-9

Biesmeijer, J. C., & de Vries, H. (2001). Exploration and exploitation of food sources by social insect colonies: A revision of the scout–recruit concept. *Behavioral Ecology and Sociobiology, 49*(2–3), 89–99. https://doi.org/10.1007/s002650000289

Bitterman, M. E., Menzel, R., Fietz, A., & Schafer, S. (1983). Classical conditioning of proboscis extension in honeybees (*Apis mellifera*). *Journal of Comparative Psychology, 97*(2), 107–119.

Camazine, S., & Sneyd, J. (1991). A model of collective nectar source selection by honey bees: Self-organization through simple rules. *Journal of Theoretical Biology, 149*(4), 547–571. https://doi.org/10.1016/S0022-5193(05)80098-0

Chandra, S. B. C., Hosler, J. S., & Smith, B. H. (2000). Heritable variation for latent inhibition and its correlation with reversal learning in honeybees (*Apis mellifera*). *Journal of Comparative Psychology, 114*(1), 86–97. https://doi.org/10.1037/0735-7036.114.1.86

Chandra, S. B. C., Hunt, G. J., Cobey, S., & Smith, B. H. (2001). Quantitative trait loci associated with reversal learning and latent inhibition in honeybees (*Apis mellifera*). *Behavior Genetics, 31*(3), 275–285.

Chandra, S. B. C., Wright, G. A., & Smith, B. H. (2010). Latent inhibition in the honey bee, *Apis mellifera*: Is it a unitary phenomenon? *Animal Cognition, 13*(6), 805–815. https://doi.org/10.1007/s10071-010-0329-6

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology, 9*(2), 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Chittka, L., Dyer, A. G., Bock, F., & Dornhaus, A. (2003). Bees trade off foraging speed for accuracy. *Nature, 424*(6947), 388. https://doi.org/10.1038/424388a

Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed–accuracy tradeoffs in animal decision making. *Trends in Ecology & Evolution, 24*(7), 400–407. https://doi.org/10.1016/j.tree.2009.02.010

Cobey, S. W., Tarpy, D. R., & Woyke, J. (2013). Standard methods for instrumental insemination of *Apis mellifera* queens. *Journal of Apicultural Research, 52*(4), 1–18. https://doi.org/10.3896/IBRA.1.52.4.09

Codling, E. A., Plank, M. J., & Benhamou, S. (2008). Random walk models in biology. *Journal of The Royal Society Interface, 5*(25), 813–834. https://doi.org/10.1098/rsif.2008.0014

Cook, C. N., Lemanski, N. J., Mosqueiro, T., Ozturk, C., Gadau, J., Pinter-Wollman, N., et al. (2020). Individual learning phenotypes drive collective behavior. *Proceedings of the National Academy of Sciences of the United States of America, 117*(30), 17949–17956. https://doi.org/10.1073/pnas.1920554117

Cook, C. N., Mosquiero, T., Brent, C. S., Ozturk, C., Gadau, J., Pinter-Wollman, N., et al. (2018). Individual differences in learning and biogenic amine levels influence the behavioural division between foraging honeybee scouts and recruits. *Journal of Animal Ecology, 88*(2), 236–246. https://doi.org/10.1111/1365-2656.12911

Couvillon, M. J., Degrandi-Hoffman, G., & Gronenberg, W. (2010). Africanized honeybees are slower learners than their European counterparts. *Naturwissenschaften, 97*(2), 153–160. https://doi.org/10.1007/s00114-009-0621-y

de Vries, H., & Biesmeijer, J. C. (1998). Modelling collective foraging by means of individual behaviour rules in honey-bees. *Behavioral Ecology and Sociobiology, 44*(2), 109–124. https://doi.org/10.1007/s002650050522

de Vries, H., & Biesmeijer, J. (2002). Self-organization in collective honeybee foraging: Emergence of symmetry breaking, cross inhibition and equal harvest-rate distribution. *Behavioral Ecology and Sociobiology, 51*(6), 557–569. https://doi.org/10.1007/s00265-002-0454-6

Donaldson-Matasci, M. C., & Dornhaus, A. (2012). How habitat affects the benefits of communication in collectively foraging honey bees. *Behavioral Ecology and Sociobiology, 66*(4), 583–592.

Dornhaus, A., Klugl, F., Oechslein, C., Puppe, F., & Chittka, L. (2006). Benefits of recruitment in honey bees: Effects of ecology and colony size in an individual-based model. *Behavioral Ecology, 17*(3), 336–344. https://doi.org/10.1093/beheco/arj036

Dreller, C. (1998). Division of labor between scouts and recruits: Genetic influence and mechanisms. *Behavioral Ecology and Sociobiology, 43*(3), 191–196.

Dyer, F. C. (2002). The biology of the dance language. *Annual Review of Entomology, 47*, 917–949.

Farina, W. M., Grüater, C., & Díaz, P. C. (2005). Social learning of floral odours inside the honeybee hive. *Proceedings of the Royal Society B: Biological Sciences, 272*(1575), 1923–1928. https://doi.org/10.1098/rspb.2005.3172

Farina, W. M., Grüter, C., & Arenas, A. (2012). Olfactory information transfer during recruitment in honey bees. In C. G. Galizia, D. Eisenhardt, & M. Giurfa (Eds.), *Honeybee neurobiology and behavior: A tribute to Randolf Menzel* (pp. 89–101). Dordrecht, The Netherlands: Springer. https://doi.org/10.1007/978-94-007-2099-2_8.

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Thousand Oaks, CA: Sage https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., Deangelis, D. L., et al. (2020). The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. *The Journal of Artificial Societies and Social Simulation, 23*(2), 7. https://doi.org/10.18564/jasss.4259

Grüter, C., & Farina, W. M. (2009). The honeybee waggle dance: Can we follow the steps? *Trends in Ecology & Evolution, 24*(5), 242–247. https://doi.org/10.1016/j.tree.2008.12.007

Guillette, L. M., Hahn, A. H., Hoeschele, M., Przyslupski, A. M., & Sturdy, C. B. (2015). Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Animal Cognition, 18*(1), 165–178. https://doi.org/10.1007/s10071-014-0787-3

Guillette, L. M., Reddon, A. R., Hoeschele, M., & Sturdy, C. B. (2011). Sometimes slower is better: Slow-exploring birds are more sensitive to changes in a vocal discrimination task. *Proceedings of the Royal Society B: Biological Sciences, 278*(1706), 767–773. https://doi.org/10.1098/rspb.2010.1669

Hart, D. D. (1981). Foraging and resource patchiness: Field experiments with a grazing stream insect. *Oikos, 37*(1), 46–52.

Hewitson, L., Dumont, B., & Gordon, I. J. (2005). Response of foraging sheep to variability in the spatial distribution of resources. *Animal Behaviour, 69*(5), 1069–1076. https://doi.org/10.1016/j.anbehav.2004.09.004

Jack-McCollough, R. T., & Nieh, J. C. (2015). Honeybees tune excitatory and inhibitory recruitment signalling to resource value and predation risk. *Animal Behaviour, 110*, 9–17. https://doi.org/10.1016/j.anbehav.2015.09.003

Johnson, L. K., Hubbell, S. P., & Feener, D. H. (1987). Defense of food supply by eusocial colonies. *American Zoologist, 27*(2), 347–358.

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. (2011). Individual-learning ability predicts social-foraging strategy in house sparrows. *Proceedings of the Royal Society B: Biological Sciences, 278*(1705), 582–589. https://doi.org/10.1098/rspb.2010.1151

Katz, K., & Naug, D. (2015). Energetic state regulates the exploration–exploitation trade-off in honeybees. *Behavioral Ecology, 26*(4), 1045–1050. https://doi.org/10.1093/beheco/arv045

Kohlmann, S. G., & Risenhoover, K. L. (1998). Effects of resource distribution, patch spacing, and preharvest information on foraging decisions of northern bobwhites. *Behavioral Ecology, 9*(2), 177–186. https://doi.org/10.1093/beheco/9.2.177

Lemanski, N. J., Cook, C. N., Smith, B. H., & Pinter-Wollman, N. (2019). A multiscale review of behavioral variation in collective foraging behavior in honey bees. *Insects, 10*(11), 370.

Liang, Z. S., Nguyen, T., Mattila, H. R., Rodriguez-Zas, S. L., Seeley, T. D., & Robinson, G. E. (2012). Molecular determinants of scouting behavior in honey bees. *Science, 335*(6073), 1225–1228. https://doi.org/10.1126/science.1213962

Lubow, R. E. (1973). Latent inhibition. *Psychological Bulletin, 79*(6), 398–407. https://doi.org/10.1037/h0034425

Mattila, H. R., & Seeley, T. D. (2007). Genetic diversity in honey bee colonies enhances productivity and fitness. *Science, 317*(5836), 362–364. https://doi.org/10.1126/science.1143046

Mazza, V., Eccard, J. A., Zaccaroni, M., Jacob, J., & Dammhahn, M. (2018). The fast and the flexible: Cognitive style drives individual variation in cognition in a small mammal. *Animal Behaviour, 137*, 119–132. https://doi.org/10.1016/j.anbehav.2018.01.011

McNamara, J. (1982). Optimal patch use in a stochastic environment. *Theoretical Population Biology, 21*, 269–288.

Mosqueiro, T., Cook, C., Huerta, R., Gadau, J., Smith, B., & Pinter-Wollman, N. (2017). Task allocation and site fidelity jointly influence foraging regulation in honeybee colonies. *Royal Society Open Science, 4*(8), 170344. https://doi.org/10.1098/rsos.170344

Nouvian, M., Mandal, S., Jamme, C., Claudianos, C., d'Ettorre, P., Reinhard, J., et al. (2018). Cooperative defence operates by social modulation of biogenic amine levels in the honey bee brain. *Proceedings of the Royal Society B: Biological Sciences, 285*(1871), 20172653. https://doi.org/10.1098/rspb.2017.2653

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.r-project.org/.

Reynolds, A. M., Smith, A. D., Reynolds, D. R., Carreck, N. L., & Osborne, J. L. (2007). Honeybees perform optimal scale-free searching flights when attempting to locate a food source. *Journal of Experimental Biology, 210*(21), 3763–3770. https://doi.org/10.1242/jeb.009563

Seeley, T. D. (1983). Division of labor between scouts and recruits in honeybee foraging. *Behavioral Ecology and Sociobiology, 12*(3), 253–259.

Seeley, T. D. (1995). *The wisdom of the hive: The social physiology of honey bee colonies*. Cambridge, MA: Harvard University Press. Retrieved from http://books.google.com/books?id=zhzNJjI2MqAC.

Seeley, T. D. (1997). Honey bee colonies are group-level adaptive units. *American Naturalist, 150*(Suppl. 1), S22–S41.

Seeley, T. D., Camazine, S., & Sneyd, J. (1991). Collective decision-making in honey bees: How colonies choose among nectar sources. *Behavioral Ecology and Sociobiology, 28*(4), 277–290. https://doi.org/10.1007/BF00175101

Seeley, T. D., Mikheyev, A. S., & Pagano, G. J. (2000). Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *Journal of Comparative Physiology A, 186*(9), 813–819. https://doi.org/10.1007/s003590000134

Sherman, G., & Visscher, P. K. (2002). Honeybee colonies achieve fitness through dancing. *Nature, 419*(6910), 920–922. https://doi.org/10.1038/nature01127

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution, 19*(7), 372–378.

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1603), 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Smith, B. H., & Burden, C. M. (2014). A proboscis extension response protocol for investigating behavioral plasticity in insects: Application to basic, biomedical, and agricultural research. *Journal of Visualized Experiments, 91*, Article e51057. https://doi.org/10.3791/51057

Smith, B. H., & Menzel, R. (1989). The use of electromyogram recordings to quantify odourant discrimination in the honey bee, *Apis mellifera*. *Journal of Insect Physiology, 35*(5), 369–375. https://doi.org/10.1016/0022-1910(89)90110-8

Staverman, A. J., & van Santen, J. H. (1941). The entropy of liquid mixtures: I. The theory of Raoult's Law. *Recueil des Travaux Chimiques des Pays-Bas, 60*(2), 76–84. https://doi.org/10.1002/recl.19410600202

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.

Tait, C., & Naug, D. (2020). Cognitive phenotypes and their functional differences in the honey bee, *Apis mellifera*. *Animal Behaviour, 165*, 117–122. https://doi.org/10.1016/j.anbehav.2020.04.023

Tanner, D. A., & Visscher, P. K. (2010). Adaptation or constraint? Reference-dependent scatter in honey bee dances. *Behavioral Ecology and Sociobiology, 64*(7), 1081–1086. https://doi.org/10.1007/s00265-010-0922-3

Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P., & Stanley, H. E. (1999). Optimizing the success of random searches. *Nature, 401*(6756), 911–914. https://doi.org/10.1038/44831

von Frisch, K. (1967). *The dance language and orientation of bees*. Cambridge, MA: Harvard University Press.

Waddington, K. D., & Kirchner, W. H. (1992). Acoustical and behavioral correlates of profitability of food sources in honey bee round dances. *Ethology, 92*(1), 1–6. https://doi.org/10.1111/j.1439-0310.1992.tb00945.x

Wolf, T. J., & Schmid-Hempel, P. (1989). Extra loads and foraging life span in honeybee workers. *Journal of Animal Ecology, 58*(3), 943–954.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2021.06.033.

Appendix

Table A1

Results of GLMM with number of forager visits to feeders as the response variable

Effect	$\chi^2{}_1$	*P*
Colony latent inhibition (LI)	27.10	<0.001
Feeder distribution	24.99	<0.001
Feeder quality	2186.90	<0.001
Colony LI × feeder distribution	4.17	0.041
Colony LI × feeder quality	292.03	<0.001
Resource distribution × feeder quality	208.72	<0.001
Colony LI × feeder distribution × feeder quality	17.38	<0.001

Colony latent inhibition, feeder distribution and feeder quality are included as fixed effects. Colony ID and date are included as random effects.

Table A2

Results of GLMM with food consumed from feeders as the response variable

Effect	$\chi^2{}_1$	*P*
Colony latent inhibition (LI)	180542.30	<0.001
Feeder distribution	26095.58	<0.001
Feeder quality	3140.19	<0.001
Colony LI × feeder distribution	7511.26	<0.001
Colony LI × feeder quality	166654	<0.001
Resource distribution × feeder quality	5491.07	<0.001
Colony LI × feeder distribution × feeder quality	4928.69	<0.001

Colony latent inhibition, feeder distribution and feeder quality are included as fixed effects. Colony ID and date are included as random effects.

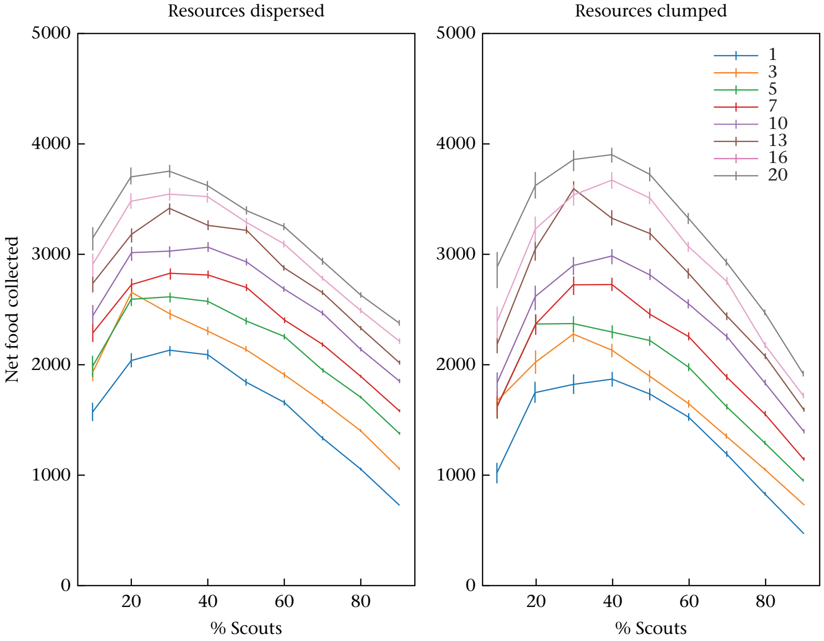

Figure A1. Sensitivity analysis of the effect of persistence on the optimal number of scouts in the simulation model. We ran the agent-based model with different values of persistence: the number of times foragers return to exploit a food patch (see persistence values in the inset). Net food was the amount of food collected at the end of the simulation minus energy expended from foraging. Colours represent different persistence values. Each line shows the mean for one value of persistence; error bars show standard error across 150 model runs.