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Sociality is a key driver of foraging ranges in bees

Highlights

- Social bees have larger foraging ranges than solitary bees
- Foraging distances increase with colony size in a food-limited environment
- Flower constancy and communication interact to increase foraging distances further
- Multiple social traits explain why social bees have greater foraging ranges

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In brief

Understanding the drivers of bee foraging ranges is important for our understanding of bee pollination services and their exposure to anthropogenic stressors. Grüter and Hayes use comparative analyses and agent-based computer simulations to show that multiple social traits explain why social bees have greater foraging ranges than solitary bees.



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Report Sociality is a key driver of foraging ranges in bees

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SUMMARY

Bees are important pollinators of wild and agricultural plants¹⁻⁵ and there is increasing evidence that many bee populations decline due to a combination of habitat loss, climate change, pesticides, and other anthropogenic effects.⁶⁻¹¹ One trait that shapes both their role in plant reproduction^{12,13} and their exposure to anthropogenic stressors is the distance at which bees forage. It has been suggested that bee sociality¹⁴ and diet¹⁵ affect bee foraging ranges, but how these traits and their potential interactions drive foraging ranges remains unclear. We analyzed flight distance data from 90 bee species and developed an agentbased model to test how social, dietary, and environmental factors affect foraging ranges. We confirm that bee sociality is positively associated with foraging range, with average-sized social bees foraging up to 3 times farther from the nest than size-matched solitary bees. A comparative analysis of social bees and computer simulations shows that foraging distances increase with colony size, supporting the hypothesis that greater foraging distances are an emergent property of increasing colony sizes in a food-limited environment. Flower constancy and communication, two traits often found in social bees, synergistically increase foraging distances further in many simulated environments. Diet breadth (oligolectic versus polylectic diet), on the other hand, does not appear to affect foraging ranges in solitary bees. Our findings suggest that multiple traits linked to bee sociality explain why social bees have greater foraging ranges. This has implications for predicting pollination services and for developing effective conservation strategies for bees and isolated plant populations.15-19

RESULTS AND DISCUSSION

Bees are central place foragers that collect floral resources to feed their brood, mainly pollen and nectar, but also nest building material, such as mud or leaves.²⁰ The distances they need to travel to collect these resources are a key determinant of a bee's energy expenditure and, as a result, are important for their overall foraging and reproductive success. For example, honeybees (Apis mellifera) produce less honey if they need to forage at greater distances²¹ and solitary bees experience a reduction in reproductive success when forced to forage farther away.^{18,22} Larger foraging distances also shorten adult lifespan^{23,24} and increase the risk of brood parasitism due to longer absences from the nest in the case of solitary bees.²⁵ Yet despite these costs, individuals of some species routinely visit food sources at impressive distances-often several kilometers from their nest-if food sources are of high quality and nearby options are scarce.²⁶ Body size has been identified as an important predictor of foraging range,^{17,27} but much of the interspecific variation in foraging range-from less than 200 m²⁸ in some species to more than 20 km²⁹ in others-remains unexplained.

There is evidence that social bees, e.g., honeybees (Apini), bumblebees (Bombini), and stingless bees (Meliponini), have larger foraging ranges than solitary species.¹⁴ One explanation

is that social bees are more likely to experience exploitation competition near their nest due to foraging nestmates, which in turn would promote foraging at greater distances as bees attempt to avoid a "halo" of low food availability in nest vicinity.^{14,30,31} In addition, sociality has allowed colonial bees to evolve communication strategies that might allow colonies to exploit distant food sources.^{26,32} Honeybees, for example, use the waggle dance to communicate food source locations and colonies are known to forage at distances of several kilometers, sometimes more than 10 km.^{26,33,34} Waggle dancing, however, is restricted to the honeybees, and it remains unknown if and how other forms of communication about food sources might affect foraging ranges. Understanding the links between sociality and foraging ranges has wider ecological and economic implications as social bees represent some of the most important and abundant pollinators of wild and agricultural plants.^{2,35,36} Another potential driver of bee foraging ranges is dietary specialization, at both the individual (e.g., flower constancy) and species level (oligolecty, i.e., specialist diet versus polylecty, i.e., generalist diet). Dietary specialization limits foraging options and could, therefore, lead to larger foraging distances as bees might need to visit isolated patches of suitable plants.¹⁵ To test how (1) sociality and (2) dietary specialization affect foraging ranges, we assessed foraging distance data of 90 bee species



Figure 1. Phylogenetically controlled analysis of foraging ranges

(A) Phylogenetic tree with divergence times in million years from now (Mya) and foraging range estimates of 71 species included in our phylogenetically controlled analyses. Squares show whether species are social, whether their diet is polylectic or oligolectic, and the method used to estimate the foraging range (see Table S1 for details). M, Melittidae; Hali, Halictidae; Col, Colletidae.

(B) Relationship between sociality, body size (IT), and foraging range (meters, log-transformed). Social species (n = 22, shown slope: y = 2.019x + 5.88) have greater foraging ranges than solitary bees (n = 24, slope: y = 1.68x + 5.09). Data are natural log-transformed.

(C) Colony size is positively associated with foraging range in 18 eusocial species. This relationship remains significant if the facultatively social *Xylocopa virginia* is included (GLS, colony size: t = 2.58, p = 0.02, n = 19). Phylogenetically independent contrasts are shown.

(D) Relationship between foraging range (i.e., max. foraging distance) and mean foraging distance in 20 species for which both estimates were available. (E) Relationship between foraging range estimates and median foraging range estimates for 17 species. Gray areas delimit 95% confidence intervals.

See also Figure S1 and Tables S1, S2, and S3.

belonging to six of the seven bee (Anthophila) families (Figure 1A; Table S1), and we developed an agent-based simulation model of bee colonies foraging in a food-limited foraging environment.

Researchers have used various methods to estimate foraging distances (Table S2), including radio and harmonic radar tracking,^{12,31} mark-release-resighting studies,^{28,37} pollen analysis,³⁸ observations on host plants,³⁹ movement of natural or artificial food sources,33,40 genotyping of worker bees,41 or waggle dance decoding.^{26,34} The most commonly used method, bee translocations (or homing; 46 species), assesses the ability of bees to find their nest after being released away from their nest (Table S2). Translocations are thought to provide good estimates of the maximum foraging range of a bee species in the tested environment.^{17,42} An important advantage of translocation studies is that they are not restricted to certain types of bees, e.g., large bees (radio tracking), eusocial bees (genotyping of workers), honeybees (waggle dance decoding), or oligolectic bees (rare pollen analysis). When we compared foraging range estimates from translocation studies with other commonly used methods, we found that the different methods correlate well (Pearson's correlation coefficient r = 0.49-0.91; Figure S1).

Using data from translocation studies, we performed a phylogenetically controlled analysis and found that social bees have larger foraging ranges than solitary bees (phylogenetic generalized least-squares model [PGLS], t = -2.21, n = 46, p = 0.03; Figure 1B). Thus, our analysis confirms the recent findings of Kendall et al.,¹⁴ using a different methodological approach (STAR Methods). Our model predicts that an average-sized social bee (intertegular distance = 2.5 mm) has a foraging range that is almost 3 times larger than that of a similarly sized solitary bee (~3,300 versus ~1,200 m). The model included body size as a covariate and confirmed the well-documented positive relationship between body size and foraging range (t = 3.12; p = 0.003).^{17,27}

One explanation for this sociality effect is that social bees experience more exploitation competition in the vicinity of their nest due to the foraging activity of their nestmates, causing foragers to search for food sources at greater distances from their nest ("halo" effect).¹⁴ This leads to the prediction that foraging ranges should increase with colony size in social bees. We tested this prediction using a phylogenetically controlled analysis that included body size as a covariate and found that colony size was indeed positively associated with foraging range estimates (Figure 1C) (PGLS, colony size, t = 3.18, p = 0.006; body size, t = 4.09, p = 0.001, n = 18). This effect remained significant when we included the facultatively social *Xylocopa virginia* (PGLS, colony size, t = 2.58, p = 0.02, n = 19). Colony size estimates ranged from less than 100 in *Lasioglossum umbripenne* or

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Figure 2. Foraging distances in simulated colonies

Average foraging distances of colonies (colony sizes range from 5 to 300) in a simulation run. Each symbol represents the mean of a single run. (A) Environments contained 3,000 high-quality and 3,000 low-quality food sources in a 2 × 2 km foraging area, but results are qualitatively identical for different abundances. If food sources replenish immediately, foragers do not experience exploitation competition and colony size does not affect foraging distances. (B) Medium refill = flowers stay empty for 20 min before offering rewards again.

(C) Slow refill = food sources stay empty for 60 min before offering rewards again. Triangles show flower constant colonies; circles represent colonies that forage randomly. Blue, colonies with communication; red, colonies without communication.

See also Table S4 and Methods S1.

Bombus pensylvanicus to more than 10,000 in *Apis mellifera* and *Trigona corvina* (Table S3). This colony size effect can explain why primitively eusocial bees, i.e., species with small, short-lived colonies founded by a single queen (e.g., *Bombus* and *Lasio-glossum umbripenne*), have shorter foraging ranges than highly eusocial bees, i.e., species with larger, long-lived colonies founded by swarming (*Apis* and stingless bees) when body size is controlled for.¹⁴

We built an agent-based simulation model (ABM) to test how colony size drives foraging distances in a food-limited environment. ABMs are a powerful tool to study the emergent properties of complex systems, such as the foraging distances of bee colonies inhabiting virtual landscapes. Under default conditions, simulated environments contained two flower species, one offering high-quality rewards, the other offering lower-quality rewards. Foragers searched for food sources using a Lévy flight search strategy^{43,44} (a type of random walk where the length of the flight segments follows a "heavy-tailed" probability distribution; STAR Methods). The simulations show that increasing colony sizes lead to larger foraging distances and that the strength of this effect depends on food availability-more specifically, on how rapidly visited food sources replenish (Figure 2). If food sources replenish more slowly, exploitation competition near the nest increases and foragers start to exploit food sources farther from their nest, in line with a "halo" effect (Figures 2B and 2C).

It has been hypothesized that communication³² and dietary specialization¹⁵ affect foraging distances. Social bees have evolved a range of recruitment behaviors to inform nestmates about the discovery of a profitable food source, including jostling runs (bumblebees,⁴⁵ stingless bees⁴⁶), thoracic vibrations

(stingless bees,⁴⁷ honeybees⁴⁸), pheromone trails (stingless bees^{46,47}), and the honeybee waggle dance.³³ While the features of these communication behaviors differ, the general function is to bias the search behavior of nestmates toward high-quality food sources.⁴⁷ Therefore, we simulated a general communication method that allowed foragers exploiting a high-quality flower type to interact with nestmates inside their nest and bias the latter's flower preference toward the same high-quality flower type (without communicating a specific location), similar to what has been found in bumblebees,⁴⁵ honeybees,³³ and most stingless bees.^{46,47} A special case of dietary specialization is flower constancy, which refers to the tendency of bees to visit flowers of one flower type during a foraging trip even if alternative options are available.^{49,50} Flower constancy relies on the capacity of bees to learn and remember rewards^{50,51} and is particularly pronounced in social bees,^{49,52} possibly because flower constancy is more beneficial in bees that communicate about food sources⁵³ and because solitary bees might need to collect food from multiple flower types during a foraging trip to achieve dietary diversity.^{54,55} In social species, on the other hand, colonies can achieve a diverse diet if different colony members specialize in different food types. Honeybees and several Trigona stingless bees, for example, have elaborate communication systems, individual foragers exhibit strong flower constancy, and colonies have a broad diet.46,50

We simulated colonies with or without communication about a high-quality food type in concert with individual foragers that were either flower constant or foraged indiscriminately. Our simulations show that in most environments, communication and flower constancy increase foraging distances synergistically (Figure 2; \sim 16%–28% increase in the environments tested in



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Figure 3. Foraging distances in relation to different food source abundances

Foraging distances of colonies consisting of 100 foragers in environments with low (3,000 flowers), medium (6,000 flowers), or high (9,000 flowers) food abundance. Two flower species were present offering either high- or low-quality rewards. Flowers differed in the time they needed to replenish their rewards after a visit (20 or 60 min). Gray dots represent the average foraging distance of a colony in a particular run (n = 30 in each condition). Blue (with communication) and red (no communication) horizontal lines and areas represent the mean and 95% confidence interval, respectively. See also Figures S2 and S3, Table S4, and Methods S1.

Figure 3). Communication alone never affected foraging distances, whereas flower constancy by itself increased foraging distances by ~10%–20% (Figures 3, S2, and S3). Flower constancy and communication cause individual foragers to focus on a subset of all available options, for example a high-quality flower type, which leads to increased competition for this flower type. As a result, foragers are more likely to search for this floral type at greater distances from their nest. Communication and flower constancy are likely to enhance each other's effects as communication causes an initial preference for a certain floral type while flower constancy causes this preference to be longlasting. This interaction is particularly strong when the high-quality flower type is less common than the lower-quality flower type, resulting in many foragers focusing on a smaller number of food sources, which drives foragers to forage at greater distances (Figures S2A and S2C). The interaction between communication and flower constancy disappears when the high-quality flower type is more common than the low-quality type (Figures S2B and S2D; see Figures S3A-S3C for a similar pattern when environments contain 4 flower species), most likely because communication allows colonies to direct their forging force toward a common flower type, thereby reducing interference competition and foraging distances. Our simulations also reveal that seemingly unrelated behavioral phenomena can increase foraging distances considerably. If we modify indiscriminate foragers so that they need more time to collect rewards than flower constant foragers because switching from one flower type to another has cognitive costs,⁵¹ the difference between indiscriminate and flower constant colonies increases considerably (Figures S3D–S3F). In this situation, cognitive constraints lead to time costs that cause indiscriminate foragers to forage at a slower tempo, thereby reducing exploitation competition and, therefore, foraging distances.

We found that food source abundance is a major driver of foraging distances (Figure 3), with decreasing food source abundance leading to larger foraging distances. Similarly, empirical studies have found that honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*) forage closer to their nest if food sources are abundant,^{31,34,56} and foraging trip durations are shorter in the solitary bee *Osmia bicornis* when foraging distances in bees are an emergent property of the interaction between innate search strategies (e.g., a Lévy flight search strategy^{43,44}), learning (e.g., an acquired preference for a certain flower type), and the foraging landscape.

One difference between our model and the empirical data is that our model estimates average foraging distances of colonies (distance between visited food sources and the nest), whereas translocation experiments estimate foraging ranges, i.e., the maximum foraging distance of a species in a particular environment. We compared foraging range estimates with estimates of average and median foraging distances in species for which all three types of estimates were available (Table S1) and found that foraging range estimates correlate strongly with average (Pearson's r = 0.84, n = 20) and median (Pearson's r = 0.77, n = 17) foraging distance estimates (Figures 1D and 1E). This suggests that average and median foraging distances are a reliable predictor of foraging ranges. Median foraging distances are slightly, but significantly, lower than average foraging distances (314 ± 447 m versus 369 ± 474 m, n = 15) (paired Wilcoxon

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Α

Foraging range [log]

5

4





Figure 4. Diet and foraging distance estimates in solitary bees

Diet specialization and foraging ranges.

(A) Estimated foraging ranges of 25 solitary bee species (12 oligolectic and 13 polylactic species) based on sightings on food sources (GLS: t = 0.87; p = 0.39). "Flower observations" combines markrelease-resighting studies and estimates based on observations on rare host plant flowers.

(B) Estimated foraging ranges of 24 solitary species (6 oligolectic and 18 polylectic species) based on translocation studies (GLS: t = -1.33, p = 0.20) (see Table S1 for food foraging range data). See also Tables S1 and S2.

test: V = 102, p = 0.015), indicating that foraging distance distributions tend to be positively skewed.

It has been suggested that oligolectic species, i.e., bees specializing on one or a small number of plant species, might have greater foraging ranges than bees with a broad (i.e., polylectic) diet as they need to locate potentially isolated host-plant patches.¹⁵ We compared foraging range estimates of oligolectic and polylectic solitary bees but found no difference in foraging range estimates (PGLS, estimates based on sightings on food sources, t = 0.87; p = 0.39; estimates based on translocations, t = -1.33, p = 0.20; Figure 4). Since foraging distances impact the reproductive success and lifespan of bees, 18,22-24 oligolectic species are likely to be under stronger selection to nest near suitable host plants than polylectic bees. The oligolectic Chelostoma rapunculi and Megachile lapponica, for example, show a strong preference to nest close to their host plants.¹⁵ This selection pressure could explain why oligolectic bees do not appear to forage at greater distances.

Taken together, our results suggest that multiple traits related to social complexity explain why social bees forage at greater distances than solitary bees. A better understanding of the drivers of bee foraging ranges is crucial for our understanding of how anthropogenic changes affect bee populations. For example, bees with smaller foraging ranges are likely to be more affected by habitat fragmentation,²⁸ while larger foraging distances might allow bees to adjust better to changes in food source availability and local habitat loss. A larger foraging range is likely to create a more constant food supply as bees have access to a greater variety of habitats containing a larger richness of plants (due to the positive species-area relationship). Bombus terrestris, for example, is thought to be very adaptable to different environments in part due to its large foraging range compared to other bumblebee species.⁵⁷ Pollinator foraging ranges are also important for plant species that are impacted by fragmentation.^{58,59} A striking example is the Amazonian tree Dinizia exelsa, a species that faces severe habitat fragmentation in its native range but thrives in fragmented habitats thanks to the pollination provided by non-native Africanized honeybees, a species with a large foraging range that has taken over the role of native pollinators in these habitats.⁵⁸ A better understanding of how biological and ecological traits shape bee foraging ranges provides an important basis for predicting pollination services¹⁶ and for the development of effective conservation strategies of isolated plant populations and specific types of bees.^{15,17-1}

STAR***METHODS**

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j. cub.2022.10.064.

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AUTHOR CONTRIBUTIONS

C.G. planned the study and collected the literature data. L.H. and C.G. planned and built the agent-based model. C.G. analyzed the data and wrote the original draft of the manuscript. C.G. and L.H. reviewed and edited the manuscript.

DECLARATION OF INTERESTS

We declare we have no competing interests.



INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR * METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data on foraging distances and body sizes	This paper	Table S1
Data on colony sizes and foraging ranges	This paper	Table S3
List of tested model parameters	This paper	Table S4
Software and algorithms		
Netlogo for agent-based model	Wilensky ⁶⁰	N/A
R version 4.1	R Development Core Team ⁶¹	N/A
Netlogo code for main model	This paper	Methods S1

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Christoph Grüter (c. grueter@bristol.ac.uk).

Materials availability

This study did not generate any new reagents.

Data and code availability

Empirical data originates from existing, publicly available publications and can be found in Tables S1 and S3. Original *Netlogo* code for the agent-based model is available in the Supplemental Information. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

All data sources reported in this paper can be found in Tables S1 and S3 and the corresponding Supplemental references.

METHOD DETAILS

Foraging range data

We collected data on (female) bee foraging ranges by combining data from earlier comparative studies^{15,17,28,40,42,62} and a literature search in Google Scholar using the search terms "bee" AND "foraging range" OR "foraging distance" OR "flight range". We found foraging distance data for 90 species (44 solitary, 44 eusocial and 2 polymorphic species) (Table S1), which is comparable to the 81 species included in Kendall et al.¹⁴ We recorded the method used to assess foraging distance (see Table S2 for details) and whether maximum, mean, or median foraging distances were estimated. We also recorded sample sizes and whether a species has a predominantly polylectic or oligolectic diet.

The most frequently used approaches are translocations (46 species), feeder/food source movement (18 species) and direct evidence of food source visits (mark-release-resighting, observations on host plants and pollen analysis, 38 species). The methods used to assess foraging ranges have different advantages and disadvantages, with some methods being feasible only for a certain species (Table S2). Kendall et al.¹⁴ classified the different methods according to whether they measure the "potential ranges" or "realized ranges". The latter is shaped by external constraints, such as food source availability or the landscape, whereas the former reflects the fundamental physiological limit in the absence of external constraints. However, this distinction is problematic as data from feeder and translocation studies (category "potential range"¹⁴) are known to be affected by various external factors, such as foraging experience,⁶³ landscape type^{64,65} and food availability.⁶⁶ We therefore decided to test the effects of sociality on foraging ranges by including data from translocation studies only. Translocations (or homing tests) can be used for most bee species and are considered a good indicator of the actual foraging range.^{17,42} We excluded data of bees that did not return on the release day (if information about return time was given).





Colony size and body size data

Colony size estimates were taken from the published literature (Table S3). We used the intertegular distance (ITD) as a measure of body size¹⁴ and averaged ITD values if multiple values were available for a species.

Phylogenetic framework

The phylogenetic framework for the comparative analysis relied on phylogenetic trees with branch lengths that are proportional to geological time. We combined phylogenetic information from Cardinal et al.⁶⁷ (Anthophila), Rasmussen & Cameron⁶⁸ (Meliponini), Ramirez et al.⁶⁹ (*Melipona*), Arbetman et al.⁷⁰ (*Bombus*), Dorchin et al.⁷¹ (*Tetraloniella*), Trunz et al.⁷² (Megachilidae), Gonzalez et al.⁷³ (Megachilidae), Haider et al.⁷⁴ (*Osmia*), Gibbs et al.⁷⁵ (Halictidae), Pisanty et al.⁷⁶ (Andrenidae), Polidori et al.⁷⁷ (*Andrena*) and Leys et al.⁷⁸ (*Xylocopa*). These trees were pruned to include only the taxa relevant for the comparative analysis (see Figure S1 for species that were included in our analysis). Sub-trees of this tree were used to answer different questions using the "*drop.tip*" function.

The agent-based model

An agent-based model (ABM) was built using NetLogo 6.1^{60} (see Methods S1 for NetLogo code). The model simulates a colony within an environment containing food sources. The agents ("bees") move in a two-dimensional square grid with 400 x 400 patches. A single patch length corresponds to 5 meters and 1 tick corresponds to 1 second. Thus, the size of the virtual world corresponds to 2 x 2 km. The nest of the colony is positioned in the center of the grid (x=0, y=0). The simulated environments contained between 1 and 4 different flower species (2 was the default) which differed in the rewards they offered.

Communication and flower constancy

Social bees have evolved different behavioral mechanisms to transmit social information and, thereby, influence the food source preferences of their nestmates. The model does not simulate a particular behavior, but a general process that causes a bias in the food preferences of nestmates after interacting with a successful forager. Foragers that provide social information about a food source type to nestmates inside their nest are called *influencers*. If colonies were flower constant, foragers would visit the flower type they encountered after leaving the nest, irrespective of the quality of the reward ("spontaneous flower constancy"⁷⁹).

We based our default parameters, such as the nest stay time (t_{nest}), flight speed (v_{flight}) and crop capacity (*Crop*) on honey bees. Other values were tested as well (see Table S4 and section Sensitivity analysis and model exploration).

Entities and state variables

Colony sizes (foragers) ranged from 5 to 300 bees (default = 100), a range which includes common colony sizes of bumble bees⁸⁰ and stingless bees.⁴⁶ Agents could assume any of the following states: (1) *generalist forager*, (2) *feeding forager*, (3) searching *forager*, (4) *returning forager*, (5) *inside-nest-worker* and (6) *influencer* (Figure S4).

Agents began the simulation in the center of the nest and as *generalist foragers*. They then moved at a flying speed of 1.4 patch/tick (v_{flight}), corresponding to a flight speed of honey bees (7 m/sec³³). Their random search behavior follows a Lévy-flight pattern (with $\mu = 1.4$ as default).^{43,44} A Lévy-flight consists of a random sequence of flight segments whose lengths, *I*, come from a probability distribution function having a power-law tail, $P(I) \sim \Gamma^{\mu}$, with $1 < \mu < 3$.⁴⁴ The inside nest speed of agents (v_{nest}) was arbitrarily chosen to be 0.1 (patch/tick). Once an agent encounters a food source, it remains on the food source for 60 ticks ($t_{flower-stay}$) under default conditions (feeding foragers).

The agent then continues to forage (searching foragers) until it reaches its desired crop threshold (see below), after which it returns to the nest (returning foragers) to unload the collected food and stay in the nest for 300 ticks ($t_{nest-stay}$).^{81,82} In the default state, only foragers visiting a high-quality food source could become *influencers* upon return to the nest. Since recruitment behaviors often depend on the food source distance,³³ with greater foraging distances lowering the probability of recruitment, the probability of becoming an *influencer* decreased with increasing distance of the last visited food patch (Figure S5). *Influencers* interacted with *inside-nest-workers* when they encountered each other on the same patch. *Influencers* encountering *inside-nest-workers* that had not foraged on high-quality food sources (see below for details about food sources) caused them to leave the nest and search for a high-quality food type.

Food sources

In the default condition, two different types of food sources could be found in the environment. The food source types differed in the rewards they offered per visit, allowing bees to recruit to the better food source. Natural flowers visited by bees offer between 0.1 and $10 \,\mu\text{L}$ of nectar per flower.⁸³ For the default condition, we chose 5 μL for the high-quality type and 2.5 μL for the low-quality type. This reward could represent an individual flower that offers a large reward or a small patch of several flowers, each offering smaller quantities, or it could represent a larger patch of flowers that is shared by several bees.

We tested different refill times (t_{refill}) for food sources: 0, 1200 and 3600 ticks. When t_{refill} = 0, food sources offered rewards again immediately after the visit of a bee. This simulates conditions under which bees would have a very high probability of finding a reward after locating a food source, which can be realistic for food patches. With t_{refill} = 3600, a flower or patch was empty for 60 minutes after it had been visited by a bee,⁸⁴ leading to intense exploitation competition among bees. The number of food sources per type in the

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simulated environment varied between 1500 (*low abundance*) and 4500 (*high abundance*). Default conditions simulated even numbers of food sources for both food source types, but we also explored uneven food source abundances (Table S4).

Apis mellifera can carry up to \sim 70 µL of nectar in their crop, but they usually carry less.^{85,86} The crop load has been shown to depend on the quality of the visited food source, with lower quality food sources leading to smaller crop loads.⁸⁵ Agents visiting the low-quality flower type foraged until their crop contained 25 µL, whereas agents visiting the high-quality food type collected 50 µL per foraging trip. Bees that choose indiscriminately had an intermediate crop capacity of 37.5 µL.

Each simulation lasted 36,000 ticks (corresponding to 10 hours), mimicking a day with good foraging conditions. We measured the average foraging distance of a colony as the average distance between the nest and the visited flowers during a simulation run. Our main questions were if the foraging distance depended on colony size, flower constancy (vs. indiscriminate choice) and communication (vs. no communication).

Sensitivity analysis and model exploration

We varied a range of factors to explore how they affected our results (see also Table S4). We tested the effects of refill time, the absolute and relative abundance of food sources, Lévy flight μ and the shape of the recruitment curve (see Figure S4). The latter two factors led to qualitatively similar results and are not shown. We performed 30 simulation runs per parameter combination. We do not provide *p*-values for formal significance testing due to the arbitrariness of the simulation number but indicate 95%-confidence intervals to facilitate visual interpretation of the data.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical tests were done with R 4.1.⁶¹ To test whether sociality, colony size and diet affect foraging ranges, we used phylogenetic generalized least squares (PGLS) models (R package *nlme*) while assuming that traits evolve under a Brownian motion model⁸⁷ with the *corBrownian* function, as implemented in the R package *ape*.⁸⁷ Phylogenetically controlled analyses are necessary to account for the non-independence of data points due to varying degrees of relatedness among species.⁸⁷ We included body size as an additional predictor due to the well-known relationship between body size and foraging range.^{17,27} Body size did not significantly interact with either sociality or colony size; the interaction was, therefore, removed for the final model. Variables were logarithmically transformed (natural logarithm) before analyses.⁸⁷