

Benefits of recruitment in honey bees: effects of ecology and colony size in an individual-based model

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Why do some social insects have sophisticated recruitment systems, while other species do not communicate about food source locations at all? To answer this question, it is necessary to identify the social or ecological factors that make recruitment adaptive and thus likely to evolve. We developed an individual-based model of honey bee foraging to quantify the benefits of recruitment under different spatial distributions of nondepleting resource patches and with different colony sizes. Benefits of recruitment were strongly dependent on resource patch quality, density, and variability. Communication was especially beneficial if patches were poor, few, and variable. A sensitivity analysis of the model showed that under conditions of high resource density recruitment could even become detrimental, especially if foraging duration was short, tendency to scout was high, or recruits needed a long time to find communicated locations. Colony size, a factor often suspected to influence recruitment evolution, had no significant effect. These results may explain the recent experimental findings that in honey bees, benefits of waggle dance recruitment seem to vary seasonally and with habitat. They may also explain why some, but not other, species of social bees have evolved a strategy to communicate food locations to nest mates. *Key words:* *Apis mellifera*, communication, foraging, individual-based model, social insects, waggle dance. [*Behav Ecol* 17:336–344 (2006)]

Recruitment to profitable food sources is a fundamental feature of the foraging strategy of many social animals. In colonial central place foragers, from social insects to birds in breeding colonies, foragers have a choice between searching for food independently or waiting at the colony in the hope that another individual may provide information about a particularly profitable resource (e.g., Brown et al., 1991; Groot, 1980; Seeley, 1995). Such information gained from conspecifics may be useful in two ways. First, foraging success of conspecifics lets unemployed foragers make an informed decision on whether it is worth foraging at all. Foraging often carries high predation risk (e.g., Goulson, 2003; Plowright and Laverty, 1984), and if little resources are available, an individual may do better by waiting inside the nest until it receives information that conditions have improved, thus avoiding risk and saving energy (Dornhaus and Chittka, 2004a). Second, information from conspecific foragers may aid in finding and selecting the most profitable, rather than just average resources, which would save time and make foraging more efficient (Brown, 1988; Frisch, 1967; Seeley and Visscher, 1988). However, when deciding to leave the nest, a forager has to weigh these benefits against the cost of waiting for such information to arrive and the chances of finding better resources independently. So what ecological or social conditions would favor information exchange over individual search? What explains the enormous diversity of information exchange and recruitment systems in central place foragers?

In social insects, foraging-related communication systems range from sophisticated to possibly none at all (Dornhaus

and Chittka, 2004a; Frisch, 1967; Hölldobler and Wilson, 1990; Maschwitz and Steghaus-Kovac, 1991; Nieh, 2004). In one of the most advanced recruitment behaviors, the honey bee waggle dance, foragers returning from a profitable food source convey information about the presence, scent, quality, and location of food sources to nest mates (Frisch, 1967; Gould, 1974). This system is unique among social insects in that it enables bees to communicate within the hive about the location of a resource patch. Many other social bee species, such as bumble bees and some stingless bees, do not communicate information about the location of resources at all (although they do transmit information about other characteristics of food sources, such as scent and quality: Dornhaus and Chittka, 2004a; Nieh, 2004). Other stingless bees, however, communicate distances of food sources using sounds or employ scent marks to guide nest mates to food sources (Biesmeijer and Slaa, 2004; Nieh, 2004). Pheromone trails to food sources are also used by many ant species as recruitment method (Hölldobler and Wilson, 1990). The recruitment systems in different social insect species thus differ in their information content and the modalities used. However, even systems that seem to transmit the same information are not necessarily equivalent. Apart from varying in efficiency (time and energy investment needed per recruit), they also vary in how potential recruits are targeted. For example, pheromone trails such as those used by ants and the waggle dance used by honey bees both communicate locations of resources. But pheromone trails are a “mass recruitment” system, and the waggle dance recruitment is signaler limited. This means that a single ant can recruit a large number of other ants with its pheromone trail: the number of recruits mainly depends on how many potential recruits are available to follow the trail while the odor persists. One honey bee, on the other hand, can only recruit a fixed number of nest mates (probably less than one per dance; e.g., Gould, 1975; Gould et al., 1970; Seeley and Towne, 1992; Tautz, 1996), independently of how

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many bees are waiting to be recruited in the hive (the same is true for tandem running in ants). This is because there is a physical limit to the number of bees that can follow another bee dancing (or a tandem run leader). In such a signaler-limited system, the number of recruits is therefore mostly determined by the number of signalers, whereas in a mass recruitment system, the number of recruits is largely determined by the number of potential recruits available.

It is not clear what factors lead to the evolution of such different recruitment strategies. For some species, benefits of communicating food source locations may not outweigh the time and energy costs of recruitment (Maschwitz and Steghaus-Kovac, 1991). Two recent studies have supported the argument that benefits may be dependent on ecology: in honey bees, benefits of communicating food locations were found to vary greatly between seasons (Sherman and Visscher, 2002) and between habitats (Dornhaus and Chittka, 2004b). Besides environmental factors, colony size may influence the benefits of certain recruitment strategies, which has been suggested in ants (Anderson and McShea, 2001; Beckers et al., 1989; Beekman et al., 2001; Jun and Pepper, 2003). However, actual colony-level benefits have not been measured for different colony sizes. Because they use a signaler-limited recruitment system, rather than mass recruitment, findings from ants will not necessarily apply to honey bees. Beekman et al. (2004) showed that large and small honey bee colonies forage at the same number of patches. It is thus not clear whether larger or smaller colonies should be more dependent on recruitment in honey bees.

Empirical studies cannot easily identify which factors determine benefits gained through recruitment. The existing studies (Dornhaus and Chittka, 2004b; Sherman and Visscher, 2002) were not designed to identify which of the factors differing between seasons or habitats caused the difference in recruitment benefits. Effects of colony size were not investigated. Similarly, comparing recruitment systems in species with differing colony sizes is confounded by the fact that most species differ in a number of other parameters as well. Therefore, we used an individual-based model of honey bee foraging to separate the influence of parameters such as resource distribution and colony size. Such a model facilitates a systematic analysis of the contribution of ecological, social, and behavioral factors, by quantifying foraging success with and without recruitment while controlling for all other factors.

METHODS

We developed a spatially explicit, individual-based model of a foraging honey bee colony, using the simulation tool SeSAM (www.simsesam.de). The simulated bees are represented in a two-dimensional space, where each individual occupies a specific location at every point in time (e.g., De Vries and Biesmeijer, 1998). An individual-based model has the advantage of allowing systematic and controlled analysis with less abstraction than that needed to make analytical models tractable (see Discussion).

In our model, bees could perform any of seven behaviors (staying inactive in the hive, searching for a food patch, flying to a known location, foraging at a food patch, returning to the hive, unloading, and dancing). The model specifies the rules according to which bees could switch between behaviors (Figure 1, Table 1). All these behavioral states and rules are taken from experimental results on honey bees (Frisch, 1967; Seeley, 1995; see also Table 1). Only the behavior of bees that were potential foragers was modeled. We modeled colonies of 1000 bees in all simulations except when investigating colony size. This is the approximate number of potential foragers in an average-sized honey bee colony (Seeley, 1985). At the start

of a simulation, the hive (containing all bees) is placed in the centre of an 8×8 km map (64 km^2). This area was chosen because more than 90% of foraging trips typically occur within 4 km of a hive (Beekman et al., 2004; Seeley, 1995; Visscher and Seeley, 1982). During the simulation, the behavioral state and variables are updated for each bee in turn (in a randomized order) at every time step. Each time step in the simulation represents 36 s, and each simulation was run for 5000 time steps. Thus, in each run, the foraging process of a honey bee colony during 50 h was simulated. This might represent 5 days of foraging, with 10 h of activity per day. We chose this interval because it is close to the length of time individual floral food sources may be open and rewarding for bees (Seeley, 1995; for longevity of individual flowers: Primack, 1985). A simulation run, then, represents the time from the appearance of one set of food sources to the time when they are likely to disappear. At the end of a simulation run, the results, such as the total amount of energy collected by the colony, are recorded. Because of the probabilistic nature of the model, at least 10 simulation runs were performed with each combination of parameter values.

Resource distribution

The first goal of the model was to study the influence of resource distribution on foraging success of a bee colony with and without the ability to communicate the locations of food sources. Resources are modeled as food patches, which can be detected by a searching bee within 25 m. These food patches could represent a flowering tree or a cluster of other flowering plants; on one foraging trip, a bee usually restricts its foraging to one such patch (Seeley, 1985). We varied the number of food patches (and thus resource density) from 32 to 2048 (in the simulated foraging range of 64 km^2). This covers a wide range of resource densities encountered by bees. The lower densities may be thought to represent tropical forest, with only one species of tree in flower at a time and very low densities of individual species (Clark 1994; Dornhaus and Chittka, 2004b). The highest number of food patches represents a density of 32 patches/ km^2 . The quality of food patches in our model is defined as the amount of nectar available for a bee to collect in one foraging trip. This was varied from 2.5 to 80 μl (the maximum capacity of the honey bee crop, Frisch, 1967), and the energy content of nectar was assumed to be 5.819 J/ μl (about 30% sugar per weight, which is a typical value, Seeley, 1985). Empirical studies show that the typical amount collected by bees from natural food sources varies mostly from 10 to 30 μl per trip (and thus per patch; Beekman et al., 2004; Roubik et al., 1986; Seeley 1985, 1995; Thom et al., 2000, Dornhaus A and Chittka L, unpublished data). Although the definition of “quality” just given thus relates to nectar volume, it can equally be thought of as representing sugar concentration or total sugar mass (incorporating concentration and volume).

In our model, patch quality (nectar standing crop) stays constant throughout a simulation run, independently of the number of bees foraging from each patch. This is clearly a simplifying assumption. However, it is not entirely clear how the distribution of foragers from one particular colony would influence patch quality. The relationship between visitation and standing crop is complicated, first because plants may vary their nectar secretion rates depending on visitation (e.g., Castellanos et al., 2002; Schaffer et al., 1979; Stone et al., 1999). But more importantly, standing crop at a particular patch may not change when the number of visitors from one particular colony decreases or increases. If the patch is also visited by competitors (from other colonies or other species of flower visitors), these may compensate by moving to or

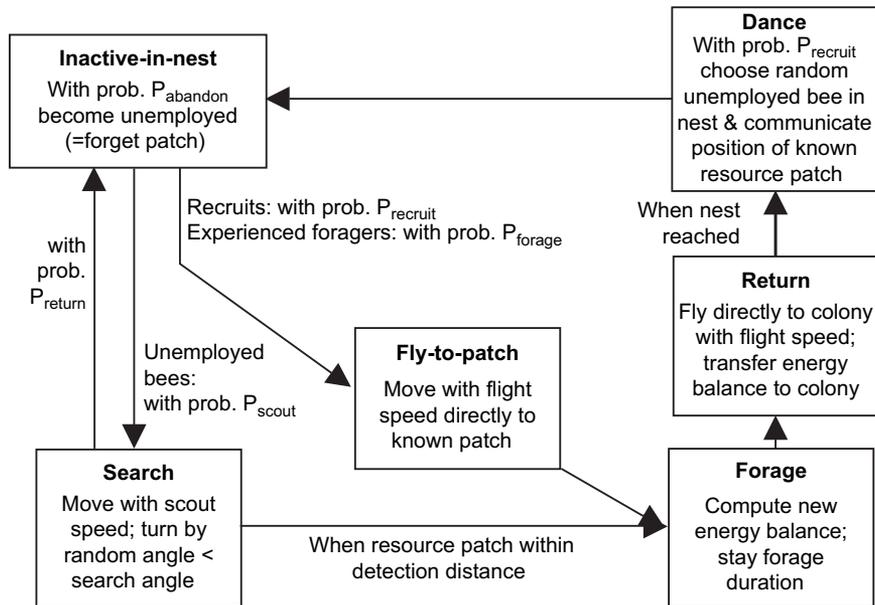


Figure 1

Schematic representation of the model of bee behavior. Behavioral states are represented as boxes, arrows indicate how agents can move from one state to another. The activity “dance” always only takes one time step; all other activities can take variable amounts of time. Bees store only one food source location in their memory and forage at only one patch per trip. Unemployed bees, foragers that know a food patch location, and recruits who have just received information about a food patch can all be in the “inactive” state but have different probabilities of leaving it. Whether a bee arrived at a food source by searching or after being recruited, it then starts to forage and potentially recruit in turn (Biesmeijer and de Vries 2001; Seeley and Visscher, 1988).

away from that patch (Goulson et al., 1998; Schaffer et al., 1979). We plan to investigate the possible effects of competitive interactions and dynamic patch qualities in a future study.

We performed 10 simulation runs for every combination of the patch densities 32, 64, 128, 256, 512, 1024, or 2048 patches in the foraging range and qualities of 2.5, 5, 10, 20, 40, or 80 μl per patch with and without recruitment. The total energy collected by the simulated colony was analyzed in a two-way ANOVA, with patch density, patch quality, and their interaction as factors. The effects of resource distribution on benefits of recruitment were analyzed together with the effects of other parameters (see Sensitivity Analysis).

We also wanted to investigate the effect of variance in food patch quality on colony foraging success and benefits of recruitment. Food patches vary in profitability (here measured as $E_{\text{res}} = \text{net energy gained/energy expended}$, Schmid-Hempel et al., 1985) even if they do not vary in intrinsic quality because patches can be at different distances from the hive. Bees expend more energy when travelling to patches at larger distances and therefore would be expected to profit from allocating foragers to the closest patches. However, the importance of allocating workers to the most profitable patches may be even greater if patches vary in the amount of nectar available. We therefore performed additional simulation runs in which the quality of each food patch was randomly chosen between 0 and 20 μl (0 and 80 μl in a second experiment). This yields an expected average food patch quality of 10 μl (40 μl). We performed 10 simulation runs each with each combination of these two average qualities, two patch densities (64 and 2048 patches in 64 km^2), and including or excluding recruitment.

Colony size

To investigate the effect of colony size, we performed simulations with 10, 100, 1000, and 10,000 bees. Because only a small percentage of individuals in a social insect colony ever forage

(Seeley, 1985), these numbers must be seen as representing much larger total colony sizes. A bumble bee colony with 10 foragers may have a total colony size of 50–100 or larger; a honey bee colony with 10,000 individuals may only contain 1000 potential foragers. Our range of simulated forager numbers thus spans a wide range of social insect colony sizes. Again, 10 simulations were performed with each combination of colony size and resource patch density (64 or 2048 patches in 64 km^2), patch quality (10 or 40 μl), and including or excluding recruitment.

Recruitment intensity

We compare colony foraging success with and without recruitment. To study situations without recruitment, the probability of recruiting (P_{recruit} in Figure 1) was simply set to 0, without changing any other aspect of the model. In the simulations with recruitment, this probability was computed as follows.

The probability of a honey bee forager successfully recruiting another bee depends on the profitability of the food source (E_{res}), the current overall nectar influx into the colony (I_{col}), and the recruitment intensity (RI), which is influenced both by the propensity of the forager to dance and the effectiveness of the information transfer (Table 1). A high nectar influx causes nectar receiver bees to be busy and thus a delay before the forager can unload, which reduces the probability that she will dance (Seeley, 1995). In our model, we assumed a simple relationship between these parameters: we calculated the probability that a returning forager will successfully recruit another bee to its food patch as

$$P_{\text{recruit}} = \text{RI} \times E_{\text{res}}/I_{\text{col}}.$$

We assumed that the probability of recruiting is independent of the number of inactive bees in the hive (signaler-limited recruitment system).

There are few quantitative empirical data on the efficiency of honey bee recruitment. Some studies have measured the probability of bees dancing by counting the number of dances performed and the number of foraging trips made by a group of bees trained to an artificial feeder (0.7–1 dances/foraging trip observed: Seeley et al., 1991; 0.8 dances/trip: Gould, 1975; 0.7 dances/trip: Tautz, 1996). Other studies have estimated the efficiency of dancing by measuring the number of recruits arriving at such feeders (0.1–0.9 recruits/dance: Gould et al., 1970; 0.3 recruits/dance: Gould, 1975; 0.25–1.25 recruits/forager/hour: Seeley and Towne, 1992; 0.7 recruits/dance: Tautz, 1996). However, artificial feeders are not like natural food sources because they provide a huge amount of food in very short time. These values are therefore likely to be overestimates of the strength of recruitment usually found in honey bees.

Nectar influx (I_{col}) was calculated as the total energy collected/simulation duration/colony size (this will always be 0 at the beginning of a simulation run; typical values at the end of the simulation are between 0.02 J/time step/bee and 1.2 J/time step/bee, depending on resource distribution). This means that bees will accept lower quality patches when not many patches have been discovered but will become more choosy when a lot of their nest mates are foraging on high-quality patches. To estimate RI, we estimated that with a high profitability ($E_{res} = 25$) and medium nectar influx ($I_{col} = 1$ J/time step/bee), a returning bee may dance with probability 0.8 and successfully recruit a nest mate with a probability of 0.5/trip on which she dances, which would give an average of 0.4 recruits/foraging trip/bee (which is close to the values given in the literature). To arrive at this value, RI has to be set to 0.016, which was therefore set as the default value for all experiments with recruitment.

However, there is considerable uncertainty attached to the estimation of this parameter. Therefore, we performed simulations with values for RI varying 6 orders of magnitude, from 0.0000016 to 0.16, which enables us to measure the impact of varying RI on foraging success. The results were used to also determine the optimal value for RI, and therefore the optimal intensity of recruitment, for various resource distributions. As mentioned above, for experiments without recruitment RI was set to 0, which means that the probability of recruitment is 0 regardless of patch quality.

RI only reflects the probability that a bee is successfully recruited to a food source. However, recruits may need considerable time to find an indicated food source and often may only find it after several attempts (Esch and Bastian, 1970; Seeley and Visscher, 1988). During these attempts to find the food source, recruits use more energy than they would need for a direct flight. This extra energy cost per recruit is incorporated into the model as R_{cost} . This therefore takes into account the costs that accrue from unsuccessful search attempts by recruits. This may also be thought of as including any cost of the dancing (recruitment) activity itself. The possibility that recruits may find another food source on the way to the one they are recruited to is not modeled.

Sensitivity analysis

In the implementation of the model, a number of parameters relating to the foraging behavior of the bees had to be estimated (Table 1). The default values taken for each of these parameters are supported by empirical evidence. Nevertheless, it is necessary to test whether the main results of the simulations are sensitive to changes in these values. We varied each parameter while the other parameters were held constant. For each new parameter value, we performed 80 simulation runs: 10 runs each for all combinations of two

patch densities (64 and 2048 patches in 64 km²), two patch qualities (10 and 40 μ l per patch), and with or without location communication (RI = 0 and RI = 0.016). Effects on foraging success were determined by using repeated-measures ANOVA for each parameter, with number of patches, patch quality, and the tested parameter, as well as all pairwise interactions, as factors, and the 10 simulation runs for each combination as repeated measures.

The relative benefits of recruitment were computed as the ratio of the average energy collected in simulations with recruitment to the average energy collected in simulations without recruitment. If one wants to study the evolution of recruitment, it is important to study the relative benefits rather than the absolute increase in energy collected. This is because, assuming that energy collected in foraging is approximately proportional to fitness, relative benefits of recruitment predict how fast recruiting colonies would invade a population of nonrecruiting colonies. To assess the impact of model parameters on relative recruitment benefits, these were analyzed in a general linear model using number of patches, patch quality, and all parameters (Table 1) as factors. All statistical tests were performed using Minitab 13 (2000, Minitab Inc., Boston, MA).

RESULTS

Resource distribution

Foraging success (the net energy collected by the colony) was strongly dependent on both resource density and quality, and these interacted significantly, both with and without recruitment (all $p < .001$; Table 1, Figure 2). Patch quality had a much higher effect than abundance, probably because flight costs are low compared to gains at high-quality patches. The relative benefits of recruitment decreased both with increasing patch number and quality (Figure 3, statistics in Table 1). There was a significant increase in foraging success with recruitment under any food patch distribution (even with 2048 patches yielding 80 μ l each: t test, $t = -41$, $p < .001$), but the potential benefits of recruiting are a 69-fold increase in net energy gain for a colony when few, low-quality food patches are available (32 patches that yield 5 μ l) and only a 1.46-fold increase with many, high-quality ones (2048 patches yielding 80 μ l).

Without recruitment, introducing variability in the quality of patches had no effect on total foraging success, although it increased its variability (for all four combinations of patch density and quality, all t test: $p > .05$ and all F test: $p < .01$; all $n = 10$). An exception here was the situation with low patch density (1 patch/km²) and high average quality (40 μ l), where variability in foraging success decreased with more variable patch qualities ($f = 4.07$, $p = .048$). With recruitment, foraging success was higher besides being more variable if patches were variable in quality (t tests: all $p < .005$, except with 1 patch/km² yielding on average 40 μ l, $t = -1.21$, $p = .29$; F tests: all $p < .0005$; all $n = 10$).

Colony size

The number of potential foragers simulated had no influence on the net energy collected per bee: there was no significant correlation between foraging success/bee and colony size for any combination of patch density and quality either without recruitment (all $r^2 < .03$, all $p > .26$) or with recruitment (all $r^2 < .06$, all $p > .13$; all $n = 40$). However, in all these situations the variability in foraging success per bee significantly decreased with an increasing number of bees per colony (Bartlett's test, all $p < .01$) except with few low-quality patches (64 patches, 10 μ l

Table 1
Parameters used in the model

	Behavioral state transition	Parameter default setting (references)	Other values tested	Effect on foraging success			
				Without recruitment	With recruitment	Effect on relative recruitment benefits	
Resource patch density		64 and 2048 patches/64 km ²	32, 64, 128, 256, 512, 1024, 2048	$F_{6,378} = 360$, $p < .001$	$F_{6,378} = 130$, $p < .001$	$F_{1,79} = 7.45$, $p = .008$	
Patch quality		10 and 40 $\mu\text{l}/\text{trip}$ (7, 11, 13)	2.5, 5, 10, 20, 40, 80	$F_{5,378} = 3637$, $p < .001$	$F_{5,378} = 22000$, $p < .001$	$F_{1,79} = 4.83$, $p = .031$	
Probability of recruiting	$P_{\text{recruit}} = \text{RI} \times E_{\text{res}}/I_{\text{col}}$	Return \rightarrow Recruit	RI = 0.016 (1–5, 9, 10, 12)	0	—	—	
Probability of abandoning a known patch	$P_{\text{abandon}} = k_{\text{abandon}}/E_{\text{res}}$	Inactive \rightarrow Inactive	$k_{\text{abandon}} = 0.5/\text{time step}$ (8, 9, 11)	1, 100, 1000	$F_{3,147} = 245$, $p < .001$	$F_{3,147} = 306$, $p < .001$	$F_{3,79} = 4.95$, $p = .003$
Probability of leaving nest to forage if patch is known	$P_{\text{forage}} = k_{\text{forage}} \times E_{\text{res}}$	Inactive \rightarrow Fly to patch	$k_{\text{forage}} = 0.007/\text{time step}$ (9)	0.0003, 1	$F_{2,110} = 38$, $p < .001$	$F_{2,110} = 104$, $p < .001$	$F_{2,79} = 0.00$, $p = 1.00$
Probability of leaving nest to forage when recruited	$P_{\text{recruit}} = k_{\text{recruit}}$	Inactive \rightarrow Fly to patch	$k_{\text{recruit}} = 0.0025/\text{time step}$ (8)	0.00025, 1	$F_{2,110} = 1$, $p = .299$	$F_{2,110} = 2633$, $p < .001$	$F_{2,79} = 0.01$, $p = .99$
Probability an unemployed bee will scout	$P_{\text{scout}} = k_{\text{scout}}$	Inactive \rightarrow Search	$k_{\text{scout}} = 0.00033/\text{time step}$ (11)	0.000033, 0.0033	$F_{2,110} = 1845$, $p < .001$	$F_{2,110} = 258$, $p < .001$	$F_{2,79} = 0.26$, $p = .77$
Probability a scouting bee will return if unsuccessful	$P_{\text{return}} = k_{\text{return}}$	Search \rightarrow Inactive	$k_{\text{return}} = 0.0025$ (8)	0	$F_{1,73} = 1845$, $p = .068$	$F_{1,73} = 0$, $p = .711$	$F_{1,79} = 0.17$, $p = .68$
Factor by which scouts move slower than foragers	Speed scouts $= k_{\text{slow}} \times \text{flight speed}$		$k_{\text{slow}} = 0.2/\text{time step}$ (8)	0.002, 1	$F_{2,110} = 64$, $p < .001$	$F_{2,110} = 357$, $p < .001$	$F_{2,79} = 0.06$, $p = .94$
Flight speed			Flight speed = 25 km/h (11)	2.5, 50	$F_{2,110} = 3$, $p = .070$	$F_{2,110} = 6$, $p = .002$	$F_{2,79} = 0.00$, $p = 1.00$
Metabolic cost of flying			Flight cost = 6.5 J/km (6)	0.65, 65	$F_{2,110} = 176$, $p < .001$	$F_{2,110} = 67$, $p < .001$	$F_{2,79} = 0.05$, $p = .95$
Time spent foraging at a patch			Forage duration = 60 min (6, 13)	6, 120	$F_{2,110} = 313$, $p < .001$	$F_{2,110} = 4888$, $p < .001$	$F_{2,79} = 0.00$, $p = .97$
Maximal turning angle while searching			Search angle = 180/time step (6)	45, 90	$F_{2,110} = 2$, $p = .122$	$F_{2,110} = 2$, $p = .12$	$F_{1,79} = 0.00$, $p = .98$
Distance at which a patch is detected when searching		Search \rightarrow Forage	Detection distance = 25 m (6)	2.5, 250	$F_{2,110} = 482$, $p < .001$	$F_{2,110} = 219$, $p < .001$	$F_{2,79} = 8.19$, $p = .001$
Energy used by recruits until communicated patch is found			$R_{\text{cost}} = 325 \text{ J}$ (2, 4, 9, 10, 12)	0, 3.25	$F_{2,110} = 0$, $p = .797$	$F_{2,110} = 3$, $p = .047$	$F_{2,79} = 0.00$, $p = 1.00$

For statistics used see Methods. One time step in the simulation represents 36 s. Probabilities that have the unit 1/time step influence the length of an activity. For example, P_{forage} determines how long foragers stay in the nest between foraging trips: every 36 s a bee in the nest leaves with probability P_{forage} . References used to estimate parameters: 1, Esch and Bastian (1970); 2, Gould et al. (1970); 3, Mautz (1971); 4, Gould (1975); 5, Seeley (1983); 6, Seeley (1985); 7, Roubik et al. (1986); 8, Seeley and Visscher (1988); 9, Seeley et al. (1991); 10, Seeley and Towne (1992); 11, Seeley (1995); 12, Tautz (1996); and 13, Thom et al. (2000).

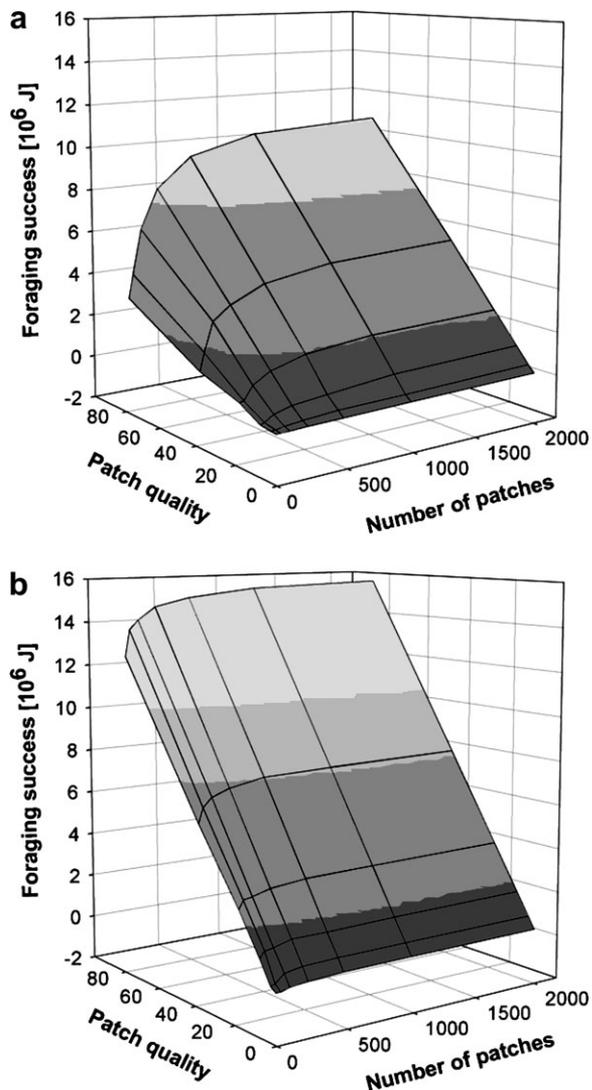


Figure 2

Average net energy gains of the simulated colony for each combination of patch quality and number of patches (10 simulation runs each; qualities: 2.5, 5, 10, 20, 40, 80 μl per patch and densities: 32, 64, 128, 256, 512, 1024, 2048 patches per 64 km^2). Foraging success (net energy gain) depends most strongly on patch quality but also on patch density. Foraging success is more variable at lower patch densities (for clarity, variation is not shown). (a) Simulations without recruitment and (b) simulations with recruitment.

per patch) without recruitment, where variability was not significantly affected by colony size ($B = 2.2$, $p = .53$).

Recruitment intensity

The optimal level of RI in terms of maximizing foraging success differed between resource distributions (Figure 4). With many (2048) resource patches available, foraging success was highest at $\text{RI} = 1.6 \times 10^{-4}$ (for both patch quality 10 and 40 μl , foraging success at $\text{RI} = 1.6 \times 10^{-4}$ was higher than at $\text{RI} = 1.6 \times 10^{-3}$ or $\text{RI} = 1.6 \times 10^{-5}$, t test, all $p < .001$, all $n = 10$). With few resource patches (1 patch/ km^2), foraging success peaked at $\text{RI} = 1.6 \times 10^{-2}$ for a patch quality of 10 μl ($\text{RI} = 1.6 \times 10^{-3}$ for patch quality = 40 μl). In this case, foraging success at higher RI values did not decrease significantly (with patch quality = 10 μl : $t = 1.5$, $p = .16$; with patch

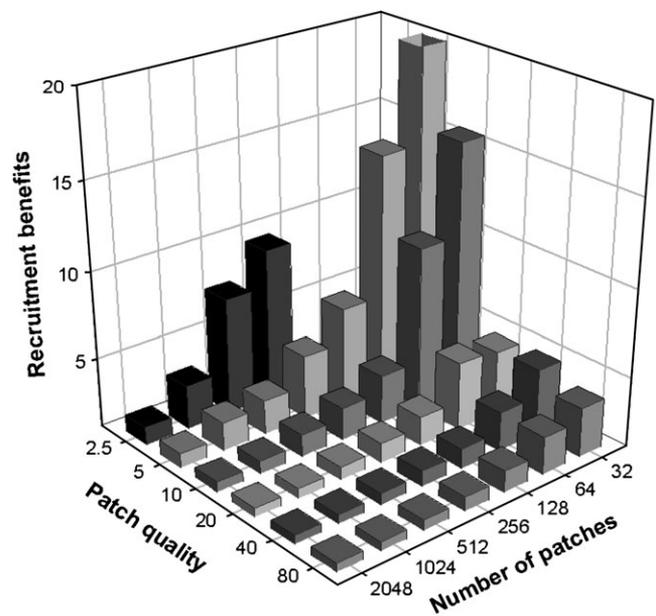


Figure 3

Relative benefits of location communication for different resource distributions (defined as average energy collected with recruitment divided by average energy collected without recruitment). Benefits increase steeply when few, low-quality resource patches are available. The graph is truncated at recruitment benefits of 20, although with 32 patches of quality 5 the relative benefit of recruitment is 69. At 32, 64, or 128 patches of quality 2.5 μl in the foraging range, average net energy gain without recruitment was negative; for these points no bars are shown.

quality = 40 μl : $t = 1.5$, $p = .17$; all $n = 10$). This means that the optimal level of recruitment was at least 10–100 times higher with fewer resources.

Sensitivity analysis

Changes in a number of the model parameters significantly affected foraging success (net energy collected), whereas others did not (Table 1). However, most of these had the same effects on foraging success with and without recruitment. Only two of the model parameters had a significant effect on the relative benefits of recruitment: k_{abandon} and detection distance (Figure 5, Table 1). With a higher probability of abandoning a known food patch (higher k_{abandon}), recruitment became more important, probably because the information about food locations could then be retained in the “collective memory” of the colony. This was particularly the case in low food patch densities. Very short detection distances made independent discovery of food patches less likely, thereby increasing the benefits of recruitment.

DISCUSSION

Our model demonstrates that potential benefits of recruitment will be very sensitive to ecological conditions, particularly the density and quality of available resources. Even though recruiting colonies collect more additional energy in absolute terms when patches are of high quality, relative benefits of recruitment decrease with increasing patch quality. Social central place foragers with a signaler-limited recruitment system, such as bees, should thus show higher levels of recruitment when resources tend to be scarce and their

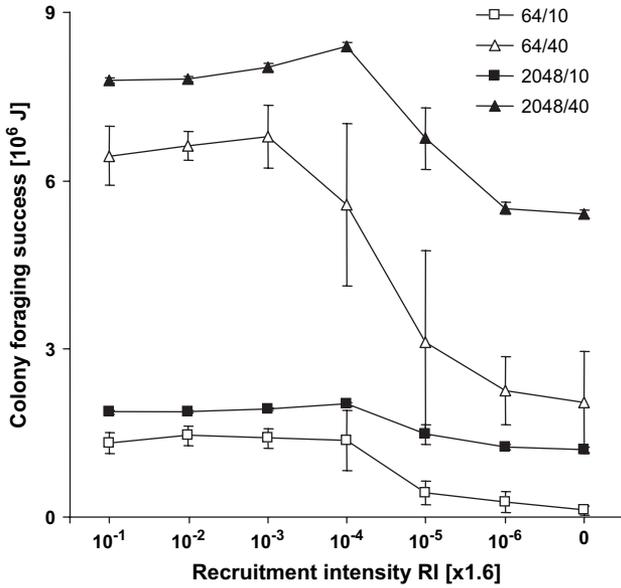


Figure 4
Foraging success as dependent on RI for four different resource distributions. In all cases, foraging success peaks at an intermediate value of RI.

quality is very variable or poor. This result may seem counter-intuitive as intuition may assume that higher absolute benefits would make evolution of a trait more likely. However, to investigate evolution of a trait, it is crucial to study its benefits relative to the ancestral trait (see Methods). This is what we have done here, by computing the benefits of foraging with recruitment relative to a strategy without recruitment.

In another individual-based model (Crist and Haefner, 1994), it was also shown that in a mass recruitment system, spatial resource distribution had a strong effect on recruitment benefits. This highlights the importance of considering

species ecology when studying recruitment evolution. The diversity of recruitment systems in social insects and other group-living animals may thus be explained by the different kinds of resources exploited by different species. It may also explain why experimental studies on honey bees found recruitment benefits to vary with season (Sherman and Visscher, 2002) and habitat (Dornhaus and Chittka, 2004b) because resource distribution is likely to change with both these factors.

Colony size, however, did not affect foraging success per individual or the benefits of recruitment in our model. Again, this may seem counterintuitive, as larger colonies have more foragers, and any improvement in foraging efficiency thus has a large effect on energy intake. However, as discussed above, to consider the evolution of a foraging strategy it is crucial to study the relative increase in foraging success. We have shown that in our model, absolute recruitment benefits increase linearly with colony size. This means that the relative increase in foraging success is the same for small and large colonies, and species with large or small colonies are thus equally likely to evolve recruitment to improve foraging success.

The effects of colony size on recruitment benefits are likely to be particularly sensitive to the kind of recruitment system studied. In a signaler-limited system, such as that modeled here, a forager can only recruit a fixed number of nest mates. If the percentage of successful scouts is independent of colony size, then so is the percentage of recruits. This is likely to be the reason that in such a system, (absolute) recruitment benefits increase linearly with colony size. However, in mass recruitment systems, such as those using pheromone trails (in some ants and stingless bees), the situation is different: one successful scout can recruit a larger number of nest mates in a larger colony. Indeed, large effects of colony size on occurrence of recruitment have been shown in mass recruiting ants, both theoretically and empirically (Beekman et al., 2001). Another factor that may influence whether colony size has an effect on optimal foraging strategy is the nature of forage patches. We assume patch quality to be in equilibrium in the habitat (see Methods), but it is possible that particularly large colonies are more likely to deplete patches if they recruit

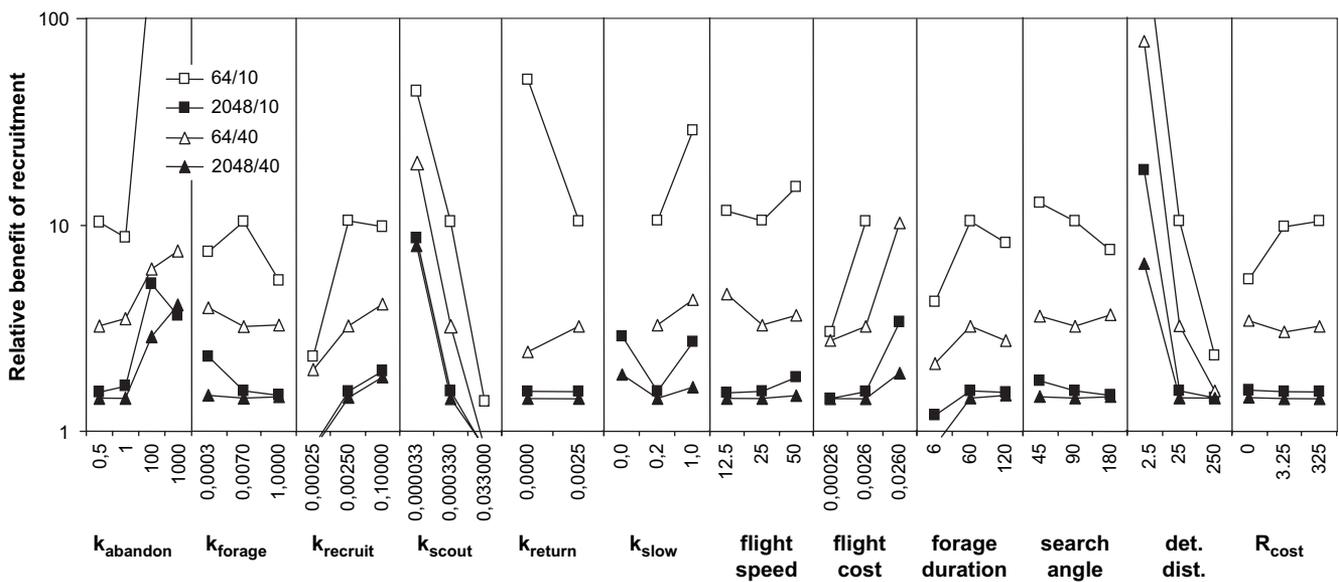


Figure 5
Sensitivity analysis shows that relative benefits of recruitment are particularly dependent on the probability of abandoning a patch ($k_{abandon}$) and the distance at which a food patch is detected (det. dist.). Relative benefits of recruitment are shown on a logarithmic axis. Values <1 indicate that recruitment was detrimental to foraging success for these parameter values. Results for four resource distribution types are shown: 64 patches in the foraging range yielding 10 μ l each, 64 patches yielding 40 μ l, 2048 patches yielding 10 μ l, and 2048 patches yielding 40 μ l.

extremely high numbers of foragers. The exact relationship between competitor density, colony size, and patch quality in a habitat thus remains to be studied, both empirically and theoretically.

We have here used an individual-based modeling approach because such models can be used to study the influence of temporal dynamics, spatial heterogeneity, or stochasticity of food availability or forager behavior (e.g., De Vries and Biesmeijer, 1998; Haefner and Crist, 1994). The advantages and uses of this method have been discussed previously (e.g., De Vries and Biesmeijer, 1998; Grünbaum, 1998; Klügl et al., 2002). Analytical models on the other hand have to be much more simplified to be tractable. For example, such models often look at a system in equilibrium (Anderson, 2001), ignoring temporal dynamics such as forager buildup, which can dramatically affect the benefits of recruitment (Deuchaume-Moncharmont et al., 2005). Empirical data suggest that the time costs of different behaviors are relevant and that a crucial function of recruitment could be the selection of particular food patches (Seeley and Visscher, 1988). Analytical models do not usually represent time costs, and many assume for simplicity that the colony forages at only one or a set of identical food patches (Anderson, 2001; Beekman et al., 2001; Deuchaume-Moncharmont et al., 2005). A disadvantage of individual-based models is that many parameter values have to be estimated; the same applies to other models that are solved numerically. In these cases, a thorough sensitivity analysis is necessary. Although this is crucial to understand the implications of modeling results to various biological systems, it is surprisingly rarely done. We have shown here that our results regarding the effect of resource distribution are robust to a change in any of the estimated parameters and that our results regarding colony size apply over a wide range of resource distributions.

We plan to use our model to investigate the benefits of other communication systems in the future, including temporal variability of food sources and competitive interactions. We believe that individual-based models such as this will become more important tools to study complex systems in the future because they can augment empirical and analytical studies with results that cannot be easily obtained by these other methods.

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