WEIGHTING WAITING IN COLLECTIVE DECISION MAKING

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ABSTRACT

Animals searching for food, mates or a home often need to decide when to stop looking and choose the best option found so far. By re-analyzing experimental data from experiments by Mallon *et al.* (2001), we demonstrate that house hunting ant colonies are gradually more committed to new nests during the emigration. Early in house hunting, individual ants were flexibly committed to new nest sites. However, when carrying to a new nest had started, ants hardly ever switched preference. Using a theoretical model based on experimental data, we test at which stage flexible commitment influences speed and accuracy most. We demonstrate that ant colonies have found a good compromise between impatience and procrastination. Early flexibility combined with later rigidity is identically effective as other strategies that include flexible commitment, but it is particularly good when emigration conditions are harsh.

1. Introduction

Decisions have consequences for the fitness of animals. One such consequence is that earlier decisions may preclude later ones. Furthermore, implementing a decision may be costly, so that it may not be profitable to reverse a decision, even if it later becomes clear that an alternative choice would have been better.

The problem of timing decisions appears in a variety of contexts (see Conradt & Roper (2005) for a review). Consider the following three examples. First, a female that sequentially encounters potential mates of different qualities might choose a threshold value for accepting a male and terminating further search (Janetos, 1980; Parker, 1983; Real, 1990). This quality threshold may be flexible and depend on the time she has spent searching. Second, a duck diving for food in a lake has to decide when to the surface to breathe. The optimal search time at the lake's floor may depend on the travel time, the probabilities of encountering more or less nutritious food, and the recovery time needed before the next dive (Houston & McNamara, 1999). Third, individuals in a group often differ in their optimal timing of activities, or in their preference for one destination over another (Krause & Ruxton 2002). This may lead to conflicts of interest between group members, and may even lead to segregation of group members into smaller groups with similar preferences (Conradt, 1998; Ruckstuhl & Neuhaus, 2002).

In this paper a decision will be identified with 'a decrease of uncertainty in an animal's behaviour' (Dawkins & Dawkins 1973). We will focus on situations in which an animal (or a group of animals) exhibits a period of exploration, after which it chooses a particular small set of behaviours to exploit one of the available options.

Decisions that have to be based on continuously incoming information may be especially problematic. Animals sometimes appear to commit the "Concorde fallacy" and base decisions only on past investments rather than overall costs and benefits (Dawkins & Carlisle, 1976; Curio 1987). Having more available options to choose from may sometimes even lead to *worse* choices (Hutchinson, 2005). When should an animal commit itself to one of the available options found thus far, and when should it remain uncommitted to any particular strategy and keep on searching?

The effect of switching strategies during the completion of a task is particularly interesting when large numbers of poorly informed individuals are involved, decision making is decentralised, when the stakes are high, and there are several multi-faceted options to choose from. The house hunting behaviour in colonies of honeybees *Apis mellifera* (Britton *et al.*, 2002; Myerscough, 2003; Seeley & Buhrman, 2001) and *Temnothorax albipennis* ants (Franks *et al.*, 2002) provide excellent opportunities to study decision making in such demanding conditions. Both social insect species regularly have to search for new nests, for instance because the old nest has deteriorated, the colony has outgrown its nest, or when new daughter colonies are founded (Michener, 1974; Winston, 1987; Partridge *et al.*, 1997). Moreover, the decision they face is particularly difficult: new nest sites may differ in several aspects, may be sparsely distributed, the whole colony is involved (actively or passively) and is vulnerable. In addition, poor individual decisions may result in colony splitting or migration to an inferior nest, which may be harder to defend against predators or may be less suited to the ants' or bees' ecology. It is therefore paramount that the emigration process as a whole is performed as swiftly and as accurately as possible (Franks *et al.*, 2002). Crucially, in *T. albipennis* ants, speed and accuracy of an emigration are in opposition (Franks *et al.*, 2003). How switching commitment between nest sites during emigrations alters the trade-off between speed and accuracy is the focal point of this paper.

In an ant colony emigration, some ants go out to find potential nest sites. Once found, the ants assess the nest's quality and start to recruit other ants to it. Many ants that actively participate in the emigration visit more than one potential nest site (Mallon *et al.* 2001), and thus acquire new and valuable information individually during the emigration. As we will see, most of these eventually

switch allegiance from the worse to the better nest site, but some also make the opposite, erroneous switch. In this paper we study the effect of the period of indecision on the trade-off between speed and accuracy of emigrations by *T. albipennis* ants (formerly *Leptothorax albipennis*) to two nest sites of different quality. We first describe, using experimental data, at which stage in house hunting switching takes place. Then we explore theoretically the value of waiting before committing to a decision; in other words, the weight that should be put on waiting. In particular, we investigate under what circumstances a lack of commitment could be detrimental.

2. METHODS

House hunting by complete colonies of the ant *Temnothorax albipennis* unfolds as follows. When the old nest is destroyed, scouting ants start to explore the surrounding area to search for a new nest. When a scout has found a potential nest site, she makes a quality assessment, and returns to the old nest to recruit other ants to the new nest site. Before commencing recruitment she uses a time delay which on average is inversely proportional to the quality of the new nest (Mallon *et al.*, 2001). This initial recruitment is typically performed using tandem runs: the recruiter ant leads the way towards the new nest site, waiting every so many steps for the recruit to catch up, teaching her the way (Franks & Richardson, 2006). When the follower has reached the nest site, she makes an independent assessment and may start to recruit others in turn. When the nest population has surpassed a certain threshold, the ants inside this nest switch from tandem-running to carrying the remainder of the colony (Pratt *et al.*, 2002). Such 'quorum sensing' is achieved by monitoring the rate at which other ants are encountered inside the nest (Pratt, 2005). Carrying is approximately three times faster than tandem running (Mallon *et al.*, 2001), but carried ants cannot learn the route as they are carried upside-down.

2.1. **Re-analysis of experimental data.** We re-evaluated behavioural data from the nest-choice experiments described in Mallon *et al.*(2001, see Fig. 1 and 2 in paper) to investigate the extent and timing of commitment switching during an emigration. In these experiments, three ant colonies (I, II and III) had all of their workers individually marked and were then allowed to emigrate to two potential nest sites. The two experimental nests differed only in their internal cavity height. It has been shown that ants of this species prefer nests with internal cavities that are not too shallow (Mallon *et al.*, 2001). The nests are called 'Poor' (with little headroom) and 'Good' (with more headroom). In all three migrations behavioural codes were assigned to all ants active during the emigration using analysis of video images (Mallon *et al.*, 2001).

To describe and later model the emigration dynamics, ants were classified as active or passive. Active ants engage in scouting, assessing or recruiting, while passive ants only take part in the emigration by being carried to a new nest. We used the following definitions for these classes.

- An ant is called a **scout** in that period of the migration in which she is not yet either an assessor or a recruiter. Ants that never enter the new nest are not taken into account.
- An ant is called an **assessor** if one of the following three conditions is satisfied:
  (1) she has entered a nest by scouting (not by being recruited) but has not yet recruited others
  (2) she has followed a tandem run to a nest, but has not yet recruited others
  (3) she has been carried to a nest and then left it again, but has not yet recruited others.
- An ant becomes a **recruiter** only if she either starts to lead her first tandem run, or if she first starts to carry an adult or brood to any nest. She is called a *tandem runner* from the time she starts leading her first tandem run to the time she carries a first brood item or passive ant. The rest of the time she is called a *carrier*. The ant remains a recruiter until the end of the emigration.

- An ant is called a **passive** ant if she is does not satisfy any of the above criteria. Effectively, this class comprises those ants that are carried into the new nest once and never leave it.

We quantified the numbers of assessors and recruiters for both nest sites over the course of the emigration (Fig. 1). Note that any ant might be committed to either nest, and that this commitment may change over time. In all three colonies the Poor nest received considerable attention, but recruitment effort was concentrated on the Good nest.

2.2. **Switching activity during the emigration.** An assessor ant was said to switch allegiance from nest i to nest j if any behaviour connected to site j was recorded when previous behaviours were connected to site i. A switching event for recruiter ants from nest i to nest j was said to take place if and only if the recruiter ant assessed and then recruited to nest j, having previously recruited to nest i. Recruiter ants for the Good nest that picked up brood or ants in the Poor nest to transport them to the Good nest were not interpreted as ants that switch allegiance.

At which stage in the emigration process are the ants flexibly committed to nest sites? We calculated the rates with which ants switched allegiance (Table 2). Switching from the Poor to the Good nest occurred significantly more often than the converse (see Table 2). Switching was particularly frequent when the ants had initially found and recruited to the Poor nest before the Good nest (colony III). Switching enhanced the divergence in the size of the pools of assessor and recruiter ants for the two nest sites, resulting in most active ants being committed to the Good nest.

2.3. **Modelling.** We set up a model to investigate how the timing of switching affects emigration performance. A previous model to explore ant emigration dynamics by Pratt *et al.* (2002) was used as a foundation. In that study, timing of switching was not taken into account. Crucially, the authors argued that switching from the superior to the inferior nest did not occur. This was based on the experimental observation that ants that had visited both sites invariably eventually recruited to the superior nest (Mallon *et al.*, 2001).

As Marshall *et al.* (2006) noted , the resulting model is very sensitive to the remaining parameter for the rate with which ants switch from nest Poor to Good, ρ_{pg}. Estimating $\rho_{pg} = 0.06$ using data from experiments in (Pratt *et al.*, 2002), Marshall *et al.* concluded that ant colonies that are given a Poor and a Good potential nest site should perform perfectly accurate emigrations with a minimal quorum threshold $T = 1$. Their response to this observation was to consider assessment noise and time costs associated with the assessment process, and to study the effect of these on the trade-off between emigration speed and accuracy (Marshall *et al.*, 2006). However, we have already seen that switches do not occur homogeneously over the course of the emigration, and that assessor ants switch considerably more than recruiters. In this paper, we therefore focus on the timing of switching, and how this influences speed-accuracy trade-offs.

We adapt the model proposed by Pratt *et al.* (2002) to study ant emigrations to two potential nest sites, Poor and Good. There are N ants in a colony, a fraction p of which are active ants. At the outset, all active ants are scouts S. These scouts go out to find new nest sites at a rate μ and become assessors A_i for nest i. These assessors turn into recruiters R_i at a rate proportional to nest quality k_i. As recruiters, the ants first perform tandem runs to nest i at rate λ_i. Once there are sufficient numbers of assessors and recruiters for nest i, the quorum is said to be met, and carrying to nest i begins at rate ϕ_i. Assessor and recruiters switch allegiance between nest i and j at rates ρ_{ij} and σ_{ij} respectively. The number of passive ants in nest i is given by P_i. The nests are denoted as follows: 0 for the old nest, and p and g for the Poor and Good nests respectively. To keep this model simple, reverse tandem runs (recruitment events in which ants are guided back to the old nest) are not taken into account.

The model is now given below. A schematic picture is presented in Figure 2.

$$
(1) \quad
\begin{cases}
\dot{S} &= -2\mu S - \big(\lambda_p(V_p, S, T, \lambda)R_p + \lambda_g(V_g, S, T, \lambda)R_g\big), \\
\dot{A}_i &= \mu S + \lambda_i(V_i, S, T, \lambda)R_i + (\rho_{ji}A_j - \rho_{ij}A_i) - k_iA_i, \\
\dot{R}_i &= k_iA_i + (\sigma_{ji}R_j - \sigma_{ij}R_i), \\
\dot{P}_i &= \phi_i(V_i, P_0, T, \phi)R_i, \\
& P_0 + P_p + P_g + A_p + A_g + R_p + R_g = N, \\
& (S, A_p, A_g, R_p, R_g, P_0, P_p, P_g)(0) = (pN, 0, 0, 0, 0, (1-p)N, 0, 0).
\end{cases}
$$

Here, $i, j \in \{p, g\}$ and $i \neq j$. Furthermore, $V_i(t)$ is the total number of assessors and recruiters in nest i at time t. To define V_i, let α be the average fraction of time an ant assessing nest i spends inside this nest, and β the average fraction of time an ant recruiting for nest i spends inside this nest, then

$$
V_i(t) := \alpha A_i(t) + \beta R_i(t).
$$

The quorum threshold mechanism, with which ants switch from recruiting through tandem running to social carrying, is incorporated by setting for $i = p, g$,

$$
\lambda_i(V_i, S, T, \lambda) :=
\begin{cases}
\lambda & \text{if } V_i < T \text{ and } S > 0, \\
0 & \text{otherwise,}
\end{cases}
$$

and

$$
\phi_i(V_i, P_0, T, \phi) :=
\begin{cases}
0 & \text{if } V_i < T \text{ and } P_0 > 0, \\
\phi & \text{otherwise.}
\end{cases}
$$

(The conditions $P_0 > 0$ and $S > 0$ are necessary to avoid these quantities becoming negative.) Note that this quorum rule is different from the one used by Pratt *et al.* (2002). In that model, only the number of recruiters were monitored. However, most of these recruiter ants are not inside the nest, while many assessor ants are. We therefore monitor the average number of assessors and recruiters inside a new nest site, V, to model the quorum rule.

A number of parameters have previously been estimated (see Table 1 in (Pratt *et al.*, 2002)), namely, $N, p, \mu, \lambda, \phi, T, k_p$ and k_g, and we take those estimates as given. Estimates of the remaining parameters in this model, α and β, and ρ_{ij} and σ_{ij}, are given in Tables 1 and 2 respectively.

We will also briefly investigate a straightforward non-linear extension to the model, specified by

$$
(2) \quad
\begin{cases}
\dot{S} &= -2\mu S - \lambda_p(V_p, S, T, \lambda)R_pS/(R_p + S) - \lambda_g(V_g, S, T, \lambda)R_gS/(R_g + S), \\
\dot{A}_i &= \mu S + \lambda_i(V_i, S, T, \lambda)R_iS/(R_i + S) + (\rho_{ji}A_j - \rho_{ij}A_i) - k_iA_i, \\
\dot{R}_i &= k_iA_i + (\sigma_{ji}R_j - \sigma_{ij}R_i), \\
\dot{P}_i &= \phi_i(V_i, P_0, T, \phi)R_iP_0/(R_i + P_0), \\
& P_0 + P_p + P_g + A_p + A_g + R_p + R_g = N, \\
& (S, A_p, A_g, R_p, R_g, P_0, P_p, P_g)(0) = (pN, 0, 0, 0, 0, (1-p)N, 0, 0).
\end{cases}
$$

Here, $i, j \in \{p, g\}$ and $i \neq j$. The underlying assumption is now that recruitment acts involve pairs of ants (scouts and recruiters, or passive ants or brood and recruiters), and that these classes are well-mixed where they meet. The number of ants of class X and Y that meet is then proportional to $XY/(X + Y)$. The two models will be tested for identical parameter settings.

Unless stated otherwise, all discussions on model results refer to the linear model.

3. SIMULATIONS AND RESULTS

We investigated the effect of switching on the speed and accuracy of simulated ant emigrations with two potential nest sites, a Good nest and a Poor nest. Here the speed of the emigration was defined by the period between the destruction of the old nest and the transportation of the last passive ant from it, and the accuracy was defined as the fraction of passive ants that were carried into the best

nest. To explore the hypothesis that increased switching improves both the speed and the accuracy of the emigrations, we performed two sets of numerical simulations. All parameters remain fixed throughout, except the switching parameters ρ_{ij} and σ_{ij}, the quorum T and the recruitment rates k_p and k_g. All simulations were performed in Matlab, using the standard `ode45` solver.

We first illustrate the effect of switching on emigration speed and accuracy using the measured mean parameter values in Table 3 (Figure 3, see caption for details). This simulation already allows us to make the following observations.

In the absence of switching, the weakness of positive feedback in the early stages of an emigration becomes apparent (Fig. 3a). Since recruiter numbers are initially low, the total number of assessors and recruiters for both nests remains practically equal, despite the quality difference between nest sites. This suggests that, in the absence of switching, the quorum threshold is reached at about the same time in both nests. This holds even for large differences in recruitment latencies, e.g. when $k_g = 10k_p$. On the other hand, even though the size of the pool of ants committed to either nest (i.e., both assessors and recruiters) is practically equal, the numbers of recruiters is not, and the majority of passive ants is still carried to the better nest. This highlights the importance of the difference in latencies to begin recruiting for nest sites of different qualities.

If assessors or recruiters do switch, the sizes of the pools of ants committed to one nest or the other differ both quickly and markedly. With more ants allocated to the better nest, the ants make more effective use of the recruitment mechanism. For these parameter values, the quorum is now reached only in the better nest if assessors switch (Fig. 3b,d), but is still met in both nests if assesors do not switch (Fig. 3a,c).

Last, note that switching has a positive influence on accuracy but not on speed. The three switching colonies all improve their accuracy either marginally or to 100%, but they take up to 10% *longer* to complete the emigration. Even though this is a relatively small change, this suggests that a better allocation of active ants to the better nest does not automatically guarantee a faster emigration.

We now put these points in a wider context, using a sensitivity analysis on parameters quorum T, recruitment latencies k_p and k_g and the four switching parameters. Setting $K = k_g/k_p$ and $M = \rho_{pg}/\rho_{gp} = \sigma_{pg}/\sigma_{gp}$, we have three degrees of freedom: T, K and M. Both K and M are measures of relative difference between the two nest sites. For each set of parameters, we performed numerical emigrations with the four strategies—no switching, switching by assessors only, switching by recruiters only, and switching by both—and determined with which strategy the highest accuracy or speed is achieved. We also calculated how much better the best strategy performed than the next-to-best one. We can make the following three observations.

First, for all parameter values, the accuracy was more sensitive to switching than speed. The non-switching strategy often did not yield the fastest emigration. On the other hand, maximum differences in speed between the best strategy and the runner up amounted to less than 5% throughout, with most simulations showing differences of less than 1%. In contrast, the best strategy on accuracy was up to 40% better than the next best one. For the rest of this discussion, we therefore focus only on the effect of switching for accuracy. These results may be found in Figure 4.

Second, when the ratio M between switching parameters increases, there is not one unique strategy that outperforms the others: several are equally good. In all such cases, both early switching (by assessors) and switching throughout gave totally accurate emigrations. In some cases, late switching also gave maximal accuracy, amounting to three optimal strategies.

Third, both when the difference between the recruitment latencies, k_i, increases (Figure 4, from left to right), and when the ratio M between switching parameters decreases, early switching prevails as the best strategy in terms of accuracy. This may seem counterintuitive since we have not assumed any costs related to switching in the model. We therefore discuss this phenomenon in some more detail in the next section.

The non-linear model, when using the same parameter settings as for the linear model, gives qualitatively identical predictions (in the sense of Fig. 4). However, one may argue that the recruitment rates have slightly different interpretations between these two models. We have therefore validated both models against the data from the nest-choice experiments in Mallon *et al.*, (2001). By varying λ, ϕ, and T using a Nelder-Mead simplex method (Nelder & Mead, 1965), whilst minimizing the L^2-error between models and data, we found best fits for these parameters for both models. The three parameters fitted to the data using the linear model differed by up to 5% from the non-linear fits for λ and T, and up to 30% for ϕ. This is less than the variation in parameter estimates for the other parameters (see Table 3). Both models therefore fit the data equally well, and furthermore give the same predictions.

3.1. **Flexible commitment may be detrimental.** In this paper we have assumed that switching costs that derive from assessment noise and time costs are negligible (but see Marshall *et al.*, 2006). Nevertheless, colonies that switched throughout the entire emigration often did not yield the best accuracies and speeds. The explanation involves two assumptions in the model:

(1) Switching is directly proportional to the number of ants that are available to switch.
(2) Switching is a bidirectional process. Switching rates from the inferior to the superior nest are greater than vice versa, but both are non-zero.

The first is a consequence of the assumption that each ant decides independently whether to switch, whilst the second is corroborated by experimental evidence (see Table 2). Now recall from eq. (1) that the recruiter population for nest i, R_i, changes over time as

$$\dot{R}_i = k_i A_i + (\sigma_{ji} R_j - \sigma_{ij} R_i).$$

If parameter values are chosen such that at some time t,

$$(3) \qquad \frac{R_g(t)}{R_p(t)} > \frac{\sigma_{pg}}{\sigma_{gp}},$$

then

$$\sigma_{gp} R_g(t) > \sigma_{pg} R_p(t).$$

In other words, when there are many more recruiter ants for the Good nest than for the Poor nest, even if a small proportion of recruiters switch from the Good nest to the Poor nest this can in total exceed the number switching to the better nest. For equation (3) to occur, recruitment numbers in the Good nest need to build up sufficiently quickly, for instance through a higher rate k_g, or for lower ratios between switching rates σ_{pg} and σ_{gp}.

For assessors we have an analogous inequality. However, in the early stages of the emigration the assessor class grows mainly by scouts finding nest sites, which occurs at equal rates for both nest sites, rather than through recruitment by tandem running. It is therefore unlikely that the numbers of assessors for the Good and Poor differ sufficiently to ever satisfy

$$\frac{A_g(t)}{A_p(t)} > \frac{\rho_{pg}}{\rho_{gp}}.$$

The resulting difference in emigration accuracy may be great: the quorum may not be reached in the inferior nest when only assessors switch, resulting in a perfectly accurate emigration. When recruiters also switch, the pools of ants committed to the two nests may be more evenly divided, so that the quorum in the inferior nest *is* reached, and some passive ants are transported to it.

4. DISCUSSION

In the absence of switching, positive feedback through recruitment is a weak mechanism to allocate more ants to better nests than to poor ones. The reason for this is that numbers of recruiters are initially low. Flexible commitment greatly augments recruitment and has a great influence on emigration accuracy, but less so on emigration speed. The most accurate emigrations were often performed by colonies that were flexibly committed to new nest sites early on, but later did not change preference.

The ants may face diverse circumstances in which to emigrate to a new nest site. The decision making mechanisms they employ thus need to be robust and perform well in a variety of conditions. The colonies discussed in this study were induced to emigrate by simply lifting the roof of the old nest. These ants have been shown to use high quorum thresholds under such conditions, and they only occasionally make mistakes when switching between nest sites (Pratt *et al.*, 2002). The ratio between their switching rates is thus high. We have seen that under such conditions, the model predicts that the timing of such switching is of less importance: any emigration strategy in which assessors are flexibly committed performs optimally.

Under adverse conditions, however, experiments have shown that ant colonies use lower quorum thresholds, thus making quicker but less accurate decisions (Franks *et al.*, 2003). The measured ratio between the two switching rates for assessor ants (see Table 2) lies in the middle of the range used in the sensitivity analysis (see Fig. 4). Under these harsh circumstances, the model thus predicts that switching by recruiters is often detrimental. The optimal strategy now is likely to be one in which ants become progressively more committed to the nests they encounter. This corresponds well with the estimates of switching rates in emigrations given in Table 3. In other words, the strategy of early switching employed by the ants during benign conditions is equally as good as any other switching strategy under these conditions, but seems particularly favourable under adverse situations.

We make two notes on the models used in this study. First, we differ in the way we have interpreted the quorum rule from the model on which we based ours (Pratt *et al.*, 2002) Our quorum rule is based on the estimated total number of ants inside a new nest, rather than on the total number of recruiters. Using the previously proposed quorum rule, however, does not alter the qualitative predictions of the model. Second, different models that fit data equally well do not always give equally good predictions (Wood & Thomas, 1999). As we have discussed, the linear and non-linear models have similar fits to the experimental data, but on top of that give the same predictions. This thus strengthens our confidence in our conclusions.

How do animals achieve a good balance between impatience and procrastination when searching for food, a home or a mate? In addition to quorum thresholds, ants use at least one other mechanism effectively to influence the accuracy of their emigrations: graded levels of commitment. This may indeed be common for many decision making organisms.

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	Good			Poor			Good			Poor		
Colony	α	S.d.	n	α	S.d.	n	β	S.d.	n	β	S.d.	n
I	0.42	0.25	40	0.31	0.20	17	0.50	0.31	29	0.22	0.12	4
II	0.36	0.26	59	0.04	0.06	16	0.29	0.17	31	n/a	n/a	0
III	0.28	0.15	52	0.10	0.11	43	0.24	0.18	34	0.02	0.01	6
Total	0.35	0.23	151	0.14	0.16	76	0.34	0.25	94	0.10	0.12	10

TABLE 1. Means and standard deviations (S.d.) of α, the fraction of time an ant assessing the Good nest or the Poor one was actually inside that nest, and β, the fraction of time an ant recruiting to nest Good or Poor was actually inside that nest. The number of assessor or recruiters ants from colony I, II and III that had actually visited the nest in question is denoted by n. Data used are from the nest-choice experiments in Mallon *et al.* (2001).

Colony	Assessor ants						Recruiter ants					
	Poor to Good			Good to Poor			Poor to Good			Good to Poor		
	mean	S.d.	n	mean	S.d.	n	mean	S.d.	n	mean	S.d.	n
I	0.0178	0.0251	18	0.0009	0.0036	38	0.0102	0.0069	8	0.004	0.0022	38
II	0.0182	0.0323	15	0.0009	0.0037	54	n/a	n/a	0	0	0	36
III	0.0299	0.0361	42	0.0099	0.0277	46	0.0142	0.0087	11	0	0	44
Total	0.0247	0.0332	75	0.0039	0.0167	138	0.0125	0.0080	19	0.0001	0.0012	118

TABLE 2. Mean switching rates, and their standard deviations (S.d.) for assessor and recruiter ants for three colonies. Switching rates were set to the mean ratio between the number of switches from one nest to the other divided by the total time an ant was an assessor or recruiter respectively for the first nest. Ants that never switched were given a switching rate of 0. For each switching rate from nest i to j, only ants that assessed nest i or recruited to it (respectively) were taken into account. Their number is denoted by n. Data used are from the nest-choice experiments in Mallon *et al.* (2001). Assessor ants from each colony switched significantly more from Poor to Good than from Good to Poor (unpaired t-tests. Col. I: $P < 0.0001$, $df = 54$, $T = -4.11$; Col. II: $P < 0.0001$, $df = 67$, $T = -3.91$; Col. III: $P < 0.005$, $df = 86$, -2.94). The same was true for recruiter ants from Colony I ($P < 0.0001$, $df = 44$, $T = -7.43$) and III ($P < 0.0001$, $df = 53$, $T = -11.11$). For Colony II an unpaired t-test could not be performed.

Parameter	Description	Mean	S.d.
N	colony size[1]	208	99
p	fraction of the colony that is active[1]	0.25	0.1
μ	rate at which scouts find a new nest (min^{-1}) [1]	0.013	0.016
λ	rate of recruitment through tandem runs, per ant (tandem runs/min)[1]	0.033	0.016
ϕ	rate of recruitment through carrying (transports/min)[1]	0.099	0.02
T	quorum threshold[1]	10	$8-30$[4]
k_p	rate at which an ant assessing Poor nest start to recruit[1]	0.015	0.006
k_g	rate at which an ant assessing Good nest starts to recruit[1]	0.02	0.008
ρ_{pg}	rate at which assessing ants switch allegiance from Poor to Good nest, per ant (min^{-1})[2]	0.0247	0.0332
ρ_{gp}	rate at which assessing ants switch allegiance from Good to Poor nest, per ant (min^{-1})[2]	0.0039	0.0167
σ_{pg}	rate at which recruiting ants switch allegiance from Poor to Good nest, per ant (min^{-1})[2]	0.0125	0.0080
σ_{gp}	rate at which recruiting ants switch allegiance from Good to Poor nest, per ant (min^{-1})[2]	0.0001	0.0012
α	mean fraction of time an ant assessing a nest spends inside this nest[3]	0.35	0.23
β	mean fraction of time an ant recruiting for a nest spends inside this nest[3]	0.34	0.25

TABLE 3. Estimated means and standard deviations (S.d.) of parameters used in the model. Estimates are from (Pratt *et al.*, 2002) (where noted) and otherwise from data gathered in (Mallon *et al.*, 2001) and analysed in this paper. [1]From (Pratt *et al.*, 2002). [2]See Table 2 for details. [3]See Table 1 for details. Rates reported here are rates averaged over three colonies. [4]Standard deviation of the quorum threshold T, as reported in (Pratt *et al.*, 2002) is unknown. Hence, its range is given.

FIGURE 1: Numbers of assessors and recruiters (top row) and total nest population inside the new nests (bottom row) during emigrations by three colonies, as described from (Mallon *et al.*, 2001). Dashed lines refer to the Poor nest, solid lines to the Good nest.

FIGURE 2: Schematic representation of the model described in equation (1). Recruiter ants are either performing tandem runs ($V_i < T$, $i = p, g$), or are carrying adults and brood ($V_i \geq T$, $i = p, g$).

FIGURE 3: Example numerical emigrations to two nest sites of differing quality, in which switching rates by assessors and recruiters vary. Dashed lines denote numbers of ants committed to (i.e., assessing or recruiting for) the Poor nest; solid lines denote numbers of ants committed to the Good nest. Titles over columns of panels indicate which ant class switched during the emigration. Note that the total number of ants committed to either nest is practically equal when neither assessors or recruiters switch (a, bottom panel), despite the quality difference between the two nests. When either assessors or recruiters switch (b–d), the pools of ants committed to the two nests quickly diverge in size, yielding higher accuracy. Parameters values are given in Table 3. Setting $M = 0.0247$ and $m = 0.0039$ (the average switching rates by assessor ants from Poor to Good and Good to Poor nests, respectively, see Table 2), we take $(\rho_{pg}, \rho_{gp}, \sigma_{pg}, \sigma_{gp}) = (0, 0, 0, 0), (M, m, 0, 0), (0, 0, M, m)$ and (M, m, M, m) for columns (a) to (d) respectively.

FIGURE 4: Strategies for which emigration accuracy was highest. For each set of parameters $K = k_g/k_p$, quorum T, and ratio $M = \rho_{pg}/\rho_{gp} = \sigma_{pg}/\sigma_{gp}$, numerical emigrations were performed for four strategies: no switching, assessors switching, recruiters switching and switching by both. Shades of gray indicate the optimal strategy. The darkest gray (with tag 'NW' for 'No Winner') corresponds with there being no one best strategy. In this case, achieved accuracy was a maximal 100%. The lighter shades designate unique optimal strategies, with 'BS' for 'Both Assessors and Recruiters Switching' and 'AS' for 'Assessors Switching'. With $\rho_{pg} = \sigma_{pg} = 0.0247$, the reverse switching rates were determined by M. Similarly, k_p was kept constant at 0.01, and k_g was varied according to K. All other parameter values were as in Table 3.
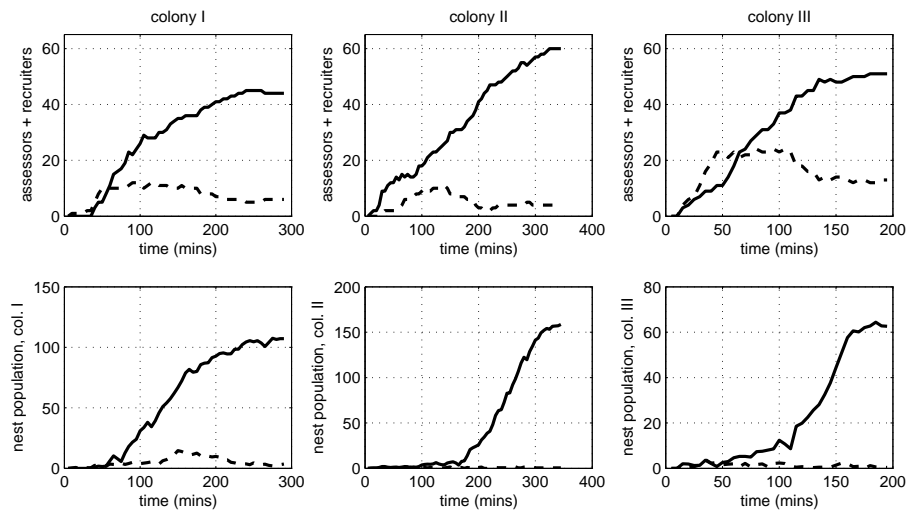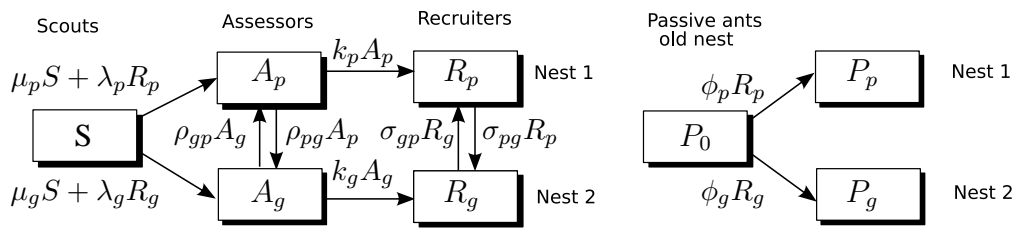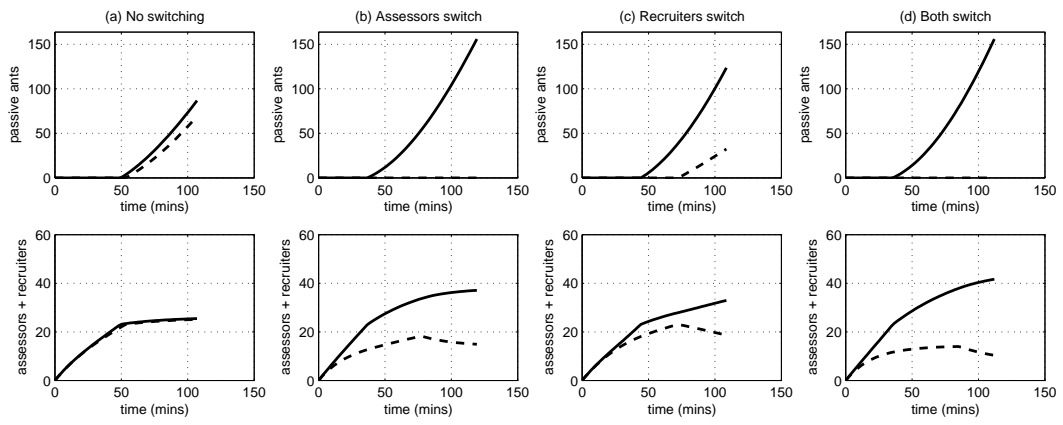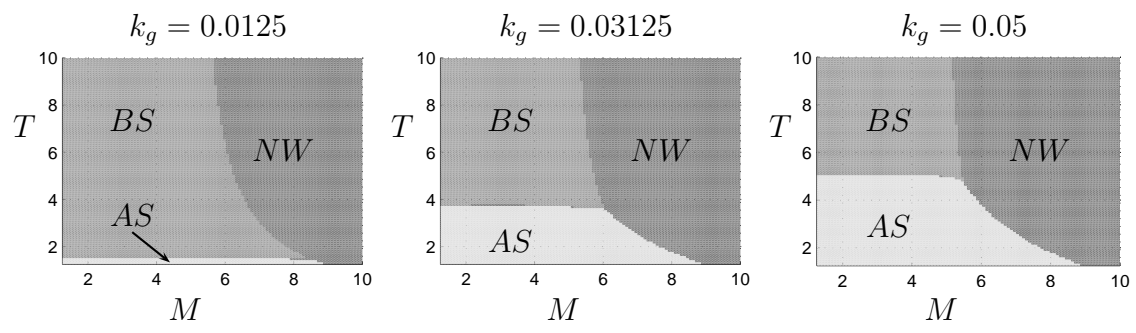
FIGURE 1

FIGURE 2

FIGURE 3

FIGURE 4