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Can ant colonies choose a far-and-away better nest over an in-the-way poor one?

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Nest choice in the ant *Temnothorax albipennis* is a model system for investigating collective decision making. Previous research has demonstrated the sophistication of this decentralized system, yet such studies have focused on binary choices in which alternative nest sites are equidistant from the colony's original nest. In nature, for example, a poor nest might be closer than a better one. Hence, to investigate the collective decision-making system of these ants further, we challenged colonies with a choice between a distant high-quality nest and a much closer and collinear poorer one. Colonies successfully emigrated to the better nest when it was two, three or even nine times further away than the collinear poorer one. Most often, colonies started emigrating simultaneously to both nests, and then they redirected all traffic exclusively to the better, more distant one. We show that this is a good strategy for minimizing exposure and risk. In principle these ants might compensate for distance effects by increasing recruitment latencies and quorum thresholds at nearby poor nests so that they are better able to find and use distant better ones. However, the simplest explanation is that scouts are more likely to begin to look elsewhere, at all stages of the decision-making and emigration process, whenever and wherever they have initially found a low-quality nest.

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Keywords: ant; collective decision; individual choice; nest site; switching behaviour; *Temnothorax albipennis*

Decision making permeates almost all animal and human behaviour. It also features prominently in mythology. For example, Buridan's ass was said to starve to death because it found itself equidistant to two equally nutritious and attractive piles of hay. Appropriate decisions depend on timely and accurate information. However, the fictional tale of Buridan's ass strikes a cautionary note: the fabulous ass was both perfectly informed and pathologically perplexed.

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House hunting in certain social insects, that is, in honeybees, *Apis mellifera*, and rock ants, *Temnothorax albipennis*, has become a model for understanding individual and collective decision making (Visscher 2007). Nevertheless, so far most experimental studies have examined choices between new nest sites that differ markedly in quality but are equidistant from the colony that needs to find a new home. We investigated collective decision making in ants that needed to find a new home and had a choice between a good distant one and a poor but nearer one. To maximize the ants' potential difficulty, we placed the poor one not only much nearer than the better one but collinearly so that the poor one was literally in the way of the better one. We conducted our experiments at a time in the ants' seasonal cycle when they should colonize a single nest (Partridge et al. 1997). Hence, this decision more closely resembles a mate choice problem than

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a foraging choice problem (see for example, Hutchinson 2005). A central place forager might decide to consume nearby food and then search further away, with its first choice having little influence on its second. However, if a female accepts a nearby poor-quality male her eggs may already have been inseminated before she encounters a more distant high-quality male. Indeed, the problem we set for the ants is similar, in principle, to the problem a female might encounter at a chorusing lek (e.g. in arthropods or anurans, see for example, Snedden et al. 1998; Greenfield & Rand 2000; Berg & Greenfield 2005). Imagine that such a female is trying to find the loudest male but a less loud male is directly between her and the better one. How does such a female avoid being 'trapped' by an option that is inferior but might appear better simply because it is nearer? Similarly, we asked whether an ant colony can find a superior nest when a poor one is not only much nearer but also directly in the path to the better one.

One advantage of social insect colonies is that they can search in many places simultaneously. In cooperatively social animals, individuals may make decisions based not only on the information they have gathered for themselves but also on the information gathered by others (Camazine et al. 2001; Seeley 2003; Conradt & Roper 2005; Couzin et al. 2005; Sumpter 2006).

We focused on the nest choice behaviour of *T. albipennis* colonies. The ability of these ants to discriminate between nests involves both individual and collective behaviours. When they need a new or better home, individual ants look for suitable nest sites. In the field, colonies nest in small flat crevices between rocks (Partridge et al. 1997); the geometry and scale of such nest sites can be approximated in the laboratory by nests made from microscope slides (Franks et al. 2002). The slides are held apart by a cardboard gasket to create a cavity of a few square centimetres with a depth of about 1 mm. The floor area, number and width of entrances, amount of headroom and illumination of the cavity can all be systematically varied in such nests. All of these characteristics, and others, are assessed by scouts initially acting independently (Franks et al. 2002, 2003b, 2005, 2006a, b, 2007a).

When individual scouts have completed their assessments, apparently using a weighted additive strategy to sum across many variables (Franks et al. 2003b), they begin to recruit nestmates to suitable new nest sites. However, they hesitate longer before recruiting to poor nest sites than to good ones (Mallon et al. 2001). Typically when they do begin recruiting nestmates they first do so by tandem running (Pratt et al. 2002). Such recruitment consists of one ant leading a single follower. A successful tandem run allows the follower to learn the route between the old nest and the new one (Franks & Richardson 2006). Tandem running continues until a quorum is built in the new nest site (Pratt et al. 2002). Quorum sizes vary with circumstances but are often in the range of 5–20 ants (Pratt et al. 2002).

Once a quorum threshold has been met, the ants typically switch from slow tandem running to carrying nestmates (Pratt et al. 2002). Carrying a nestmate is three times quicker than leading one in a tandem run (Pratt et al. 2002; Franks & Richardson 2006). Thus the switch from tandem running to carrying is an important factor for the speed of an emigration. Quorum thresholds are often sufficiently high that it is unlikely that one tandem leader could have recruited all of the ants to make the quorum. Hence, high quorum thresholds imply that more than one scout has found a given nest and deemed it suitable. Thus, quorums, in effect, facilitate pooling of separate assessments into a collective decision (Franks et al. 2002; Pratt et al. 2002). However, the quorum threshold also influences the number of ants that have been led in tandem runs, and hence have been able to learn the route between the old nest and the new one (Franks & Richardson 2006). Carried ants seem to be unable to learn the route (Pratt et al. 2002). In this way the quorum threshold also influences how many ants can be active participants in an emigration and can carry their more passive nestmates to the new nest site (Planqué et al. 2007a, b).

There are speed versus accuracy trade-offs in the house-hunting decisions of *T. albipennis* ants (Franks et al. 2003a). If their current nest is intact and still habitable and they discover a sufficiently better one, they will emigrate to it, to move to improve (Dornhaus et al. 2004). Under such circumstances, they use a very high quorum threshold, as if they were involving many individuals to ensure that a nonemergency emigration is likely to be worthwhile (Dornhaus et al. 2004). If they are currently homeless and conditions are particularly harsh they often use a very low quorum threshold or simply make individual decisions to recruit to any suitable nest. Such quick individual decision making is more errorprone than slower collective decision making (Franks et al. 2003a).

These ants are not only good at choosing the better of two equidistant nests but they can also choose the best among an array of as many as seven poorer alternatives (Franks et al. 2006a). Even when carrying to a nest site has begun, individual ants may continue to search for better alternatives (Franks et al. 2007b). Furthermore, when given the opportunity to learn about a poor nearby nest for a week, these ants are able to discriminate against such familiar mediocrity and when they are homeless they focus their search elsewhere possibly to maximize their chances of finding something better (Franks et al. 2007b).

We examined whether the decision-making abilities of *Temnothorax albipennis* ant colonies are such that they can choose a good distant nest over a poor one that is not only much closer but is exactly in the path to the better nest. In the field, when their old nest is destroyed, one might expect these ants to search in all directions for a new nest. However, colonies of *T. albipennis* are typically small with a median of about 100 workers (Franks et al. 2006a) and only a minority of such workers search for a new nest (Franks et al. in press). So, by chance, a colony might find a more distant new nest before finding a nearer but poorer one. In our laboratory experiments, we wished to test the decision-making power of these ants by presenting them with a design in which they were much more likely to find the poor nest before they found the better one. Hence, we used narrow arenas and put the poor nest directly in the path to the better one. In other words, we

wished to present the ants with a severe test in which 'good news' of a better nest is always likely to be late. Britton et al. (2002) have explored through mathematical models how honeybees are able to choose a better nest after first discovering poorer ones. Franks et al. (2007c) have examined through experiments how *T. albipennis* can redirect emigrations to better nests even when they have already begun to emigrate to poorer ones. However, the design we used in this study to maximize interference, with collinear nests, to the best of our knowledge, has never been used before.

METHODS

Experimental Colonies

We collected 18 *T. albipennis* ant colonies on 30 September 2006 and 18 on 10 January 2007 from the Dorset coast, U.K. Eleven colonies from each collection had a queen and all contained brood at various stages of development (Franks et al. 2006a). Colonies were housed in the laboratory in nests constructed from a cardboard perimeter placed between two (75 × 50 mm) glass microscope slides to form a cavity (50 × 33 mm and 1.8 mm high) with a single entrance 8 mm long and 2 mm wide in one of its longer sides. Each nest was placed in a large petri dish (220 × 220 mm and 17 mm high) with Fluon-coated walls to prevent the ants escaping. Within these arenas, colonies were provided with a water tube and fed ad libitum with dead *Drosophila* and honey solution once a week.

We used another 15 *T. albipennis* colonies, collected from the same field site on 29 September 2007 and cultured in the same way, to test whether ant colonies have intrinsic preferences for near or far collinear nests of the same quality.

Experiments

We carried out four main procedures: experiments 1, 2, 3 and a control C. In experiments 1–3, colonies were offered a choice of two nest sites: a good and a poor one. In the control, C, the good and poor nests were presented separately. Both types of nest had a cavity measuring 50 × 33 mm and 1.8 mm high. However, the poor nest had an entrance 4 mm wide and was not protected against the light, whereas the good nest had an entrance 2 mm wide and was covered with a red filter. Each experiment was carried out within a large rectangular arena (see below) with walls coated in Fluon. This arena remained in the same position on a low-vibration bench in the centre of the laboratory throughout all trials and was kept under constant lighting conditions and temperature. Great care was taken to ensure minimal disturbance to the ants.

For experiment 1, 12 colonies, from the 18 collected in September 2006, were randomly selected for recording full dynamic data. For the remaining six colonies, we recorded only the overall choice after 24 h. The same 12 colonies were used in experiment C, run in the same order as experiment 1 to ensure consistent intertrial periods. In experiment 2, we collected full data from all 18 (September 2006) colonies, again run in the same order as before. Experiment 3 involved the January 2007 colonies.

In addition to the above four procedures, we tested whether these ants have intrinsic preferences for closer or more distant collinear nests with the 15 colonies collected in September 2007.

Treatments

In experiment 1, colonies were offered a choice between a poor nest at 30 cm and a good nest at 60 cm in an arena with area of 80 × 16.5 cm (Fig. 1a). Colonies were induced to emigrate from their current nest by removing its top glass slide, which was then placed upside down directly in front of the original nest. This started the experiment and the number of adults and brood in each of the two alternative nest sites was subsequently recorded every 5 min. Recording continued until emigrations were complete, or for 3 h in the case of incomplete emigrations. Total emigration time was recorded once all brood had been moved out of the old nest. The time (min) of the following events was also recorded for each nest (poor and good): (1) first discovery; (2) first tandem run; and (3) first carrying. Discovery was defined by an adult scout fully entering the nest in question via the nest entrance. For a successful tandem run both leader and follower had to enter the nest fully while maintaining contact. A carrying event was recorded if an actively participating ant entered the nest and placed a nestmate or a brood item somewhere within that nest. After 24 h, the total number of adults and brood in each of the alternative nest sites was again recorded, indicating the colony's overall choice, before the colony was returned to its original petri dish. Colonies were considered to have split if brood were present in more than one nest at 24 h. After each trial, arenas were washed and cleaned with water and then alcohol. New nests were provided for subsequent trials.

Experiment C (conducted to provide baseline data for experiment 1) used the same arena as detailed above. Colonies were not given a binary choice; instead the emigration dynamics in the presence of either the poor nest (30 cm) or the good nest (60 cm) were recorded in separate trials (Fig. 1b). This procedure was counterbalanced, with half the colonies emigrating to the poor nest first (subsequently completing trials to the good nest), while the other half emigrated first to the good one. Data were collected as in experiment 1.

In experiment 2, the distance of the good nest was increased to 90 cm. To accommodate this, an arena with area 180 × 18 cm was used (Fig. 1c), placed in the same position on the low-vibration bench. Recordings were taken as in experiment 1. Owing to the extra distance, the experiment proceeded for 4 h (or until emigrations were complete).

In experiment 3, the distance to the good nest was increased further to 285 cm (Fig. 1d). The number of adults in the two alternative nest sites was recorded every hour for 6 h, and the presence of brood was indicated (affirmative or negative). A final recording taken at 24 h confirmed the colony's choice. No other dynamic data were recorded.

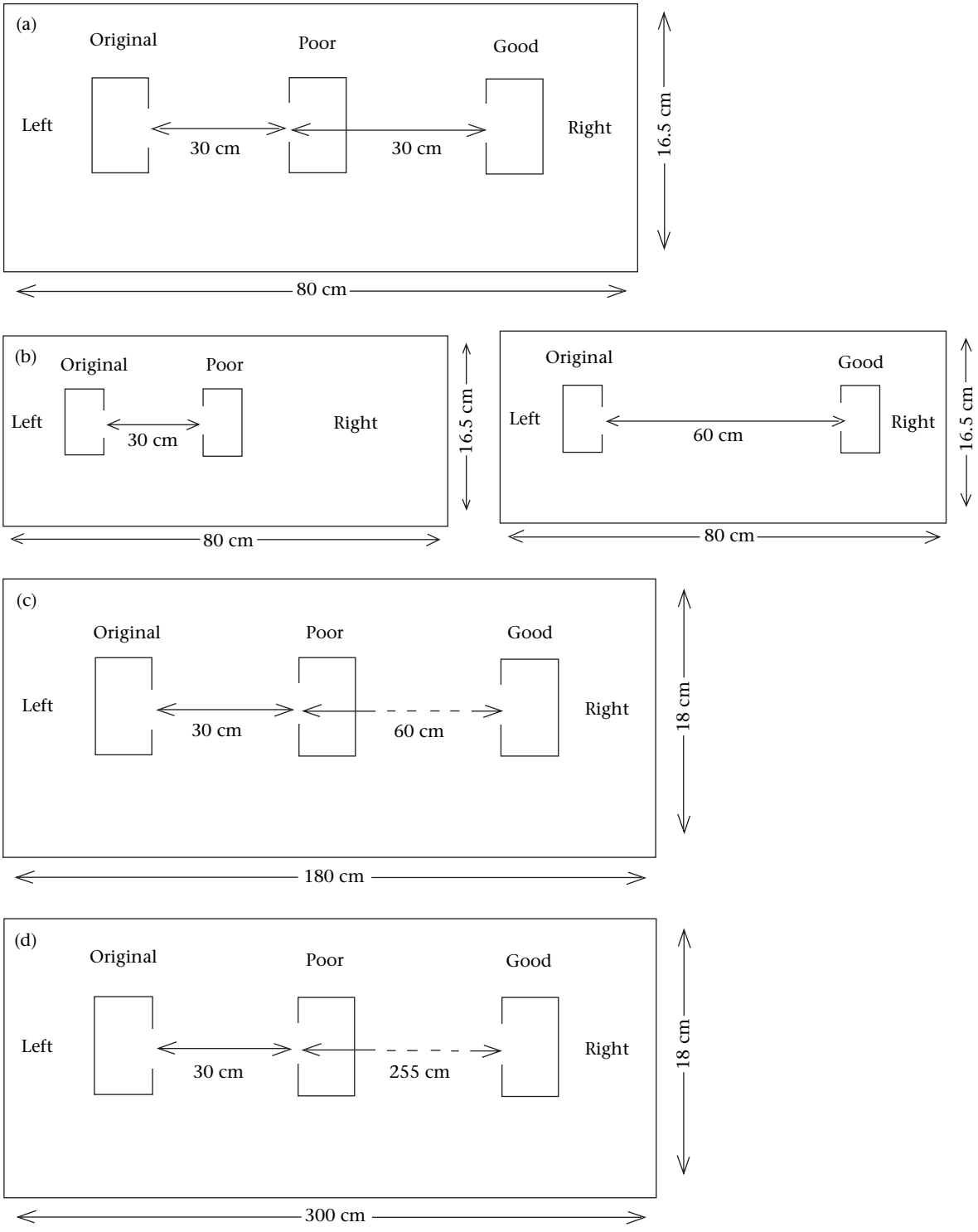


Figure 1. Experimental set-up for each of the four experiments with a poor and/or a good nest: experiments (a) 1, (b) C, (c) 2 and (d) 3. The nests are not drawn to scale. They are 75 × 50 mm. Distances between nests are measured entrance to entrance. The arena was made out of Perspex in experiments 1 and C and plastic in experiments 2 and 3.

In the test for whether ants have an intrinsic preference for closer or more distant collinear nest sites, the 15 colonies were presented with a choice between two collinear poor nests: one at 30 and one at 120 cm in an arena measuring 180 × 18 cm. The poor nests each had a cavity measuring 50 × 33 mm and 1.8 mm high, an entrance 1.5 mm wide and a clear acetate lid, and they were not protected against the light by a red filter. The orientation of the arenas was varied across trials. A trial commenced with the removal of

the lid of the old nest. Nest choice was recorded after 24 h.

Analysis

To analyse the binary choice of colonies we used a two-tailed binomial test with a probability of success of 0.5 for each trial.

We used the term 'staged emigration' for emigrations to the good nest that also involved some carrying of adults or brood to the poor nest. In some of these staged emigrations, colonies first moved entirely into the poor nest before redirecting those ants in the poor nest to the good one. However, in most staged emigrations the ants moved adults and brood simultaneously to both nests before completely abandoning the poor one in favour of the better nest (Fig. 2a). We use the term 'direct emigration' for emigrations that proceeded to the good nest exclusively (Fig. 2b).

For the analysis of the variables 'rate of population increase', 'discovery time', 'time to first tandem run' and 'time to first carrying' we applied general linear models (GLMs) with two factors. One of the factors was 'experiment' with either two levels (1 and 2) or three levels (C, 1 and 2). The second factor was either 'emigration type' (two levels: staged and direct) or 'nest type' (two levels: good and poor). For post hoc analyses we used a series of Tukey tests.

We estimated the rate of population increase in a new nest from the slope of a linear regression model fitted to the linearized logistic growth model representation (Krebs 1985) of the relation between the number of ants in a nest and time. To calculate the variables time to first tandem run and time to first carrying we took discovery time as time zero because discovery is a distinct 'nonsocial' phase of the emigration process that is independent of nest quality. Furthermore, for the variable time to first carrying we also subtracted time to first tandem run. The variables discovery time and time to first tandem run had positively skewed distributions and we used a log transformation to normalize them.

All GLMs that showed significant effects fitted well with R^2_{adj} ranging between 27.83 and 70.56% and P values from Anderson–Darling normality tests for residuals ranging between 0.207 and 0.894. An additional random factor 'colony' was also included in each of the models. In three of them, this factor was not significant and was excluded from their final versions. In one of these three models, the factor colony became nonsignificant after the removal of a single outlier: the very high value of the only data point for colony 14 (experiment 2). Its removal did not change qualitatively the effect of the other two factors in the model or its overall fit. In the remaining model, with response variable discovery time, the factor colony had a significant effect ($F_{17,60} = 3.38$, $P < 0.001$), which was due to the slow performance of two colonies in experiment 2.

Data were not always available for all response variables for all colonies in all experiments (Table 1) because of late emigrations (and hence lack of dynamic data) or direct emigrations (and hence lack of data for the poor nest).

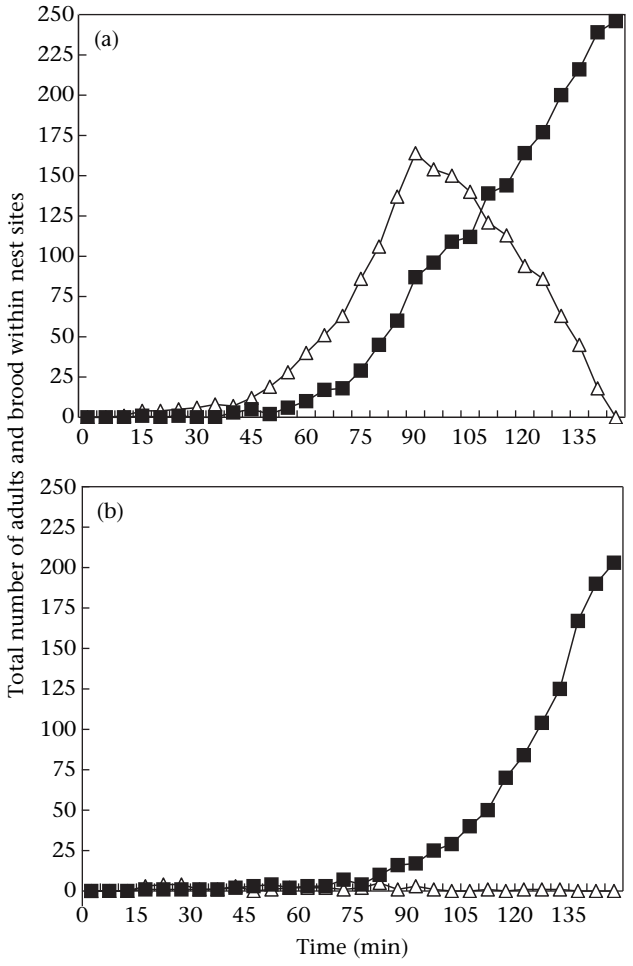


Figure 2. Example of an emigration of each of the two types: (a) staged and (b) direct, both observed during experiment 1. The emigration process is depicted in terms of the total number of adults and brood recorded within alternative nest sites at 5 min intervals. △: Poor nest; ■: good nest.

RESULTS

Choice Between Distant Good and Near Poor Nests

Colonies chose the distant good nest over the poor alternative even when the good nest was more than nine times further away. Thus, all 18 colonies emigrated to the good nest within 24 h when the good nest was 60 or 90 cm away (experiments 1 and 2, two-tailed binomial test: $P < 0.0001$ in each case). When the good nest was 285 cm away, 16 of 18 colonies emigrated to the good nest within 24 h (experiment 3, two-tailed binomial test: $P = 0.001$). The overwhelming choice of the good distant nest was not due to the ants having any intrinsic preference for a more distant nest because when both the near and distant collinear nests were of identical quality, 14 of the 15 colonies emigrated to the near nest and one to the distant nest (experiment with two poor nests; two-tailed binomial test, $P < 0.001$). This clearly shows that

Table 1. Sample sizes for the experiments on nests of different quality

Measurement	Experiment				Total sample size
	1, with colonies 1–18	C, with colonies 1–12	2, with colonies 1–18	3, with colonies 19–36	
Nest choice	18	N/A	18	18	54
No. of staged and direct emigrations	12	N/A	16	16	44
Rates for staged versus direct emigrations	12	N/A	15	N/A	27
Rates for new nest	12 G	12 G+11 P	16 G	N/A	51
Discovery time	12 G+12 P	12 G+11 P	18 G+18 P	N/A	83
Time to first tandem	11 G+10 P	10 G+9 P	15 G+14 P	N/A	69
Time to first carrying	12 G+11 P	12 G+11 P	17 G+15 P	N/A	78

G: good nest; P: poor nest.

all else being equal, the ants choose a near nest. The advantage of such a choice would be to minimize the emigration time and their exposure.

Direct Versus Staged Emigrations

Only one-third of the emigrations to the good nest were direct. The majority were staged, that is, the colonies involved emigrated to the good nest 'via' the poor nest (chi-square test for goodness-of-fit with the Yates correction for continuity: $\chi^2_1 = 5.114$, $P < 0.05$; pooling after homogeneity chi-square test: $\chi^2_2 = 1.650$, $P = 0.438$; Table 2, Fig. 2).

Pros and Cons of Direct and Staged Emigrations

The rate of population increase in the good nest in direct emigrations was significantly higher than in staged emigrations over both experiments (GLM: $F_{1,23} = 4.44$, $P = 0.046$; Fig. 3), although not for each experiment individually (Tukey test: experiment 1: $T = 0.948$, $P = 0.779$; experiment 2: $T = 2.213$, $P = 0.150$). There was also a significant main effect of distance to the good nest ($F_{1,23} = 12.72$, $P = 0.002$; Fig. 3; see below) but no interaction between emigration strategy and distance to the good nest ($F_{1,23} = 0.37$, $P = 0.549$; Fig. 3).

However, although direct emigrations were quicker, staged emigrations should be safer because the total exposure time for transported items during a staged emigration should only be the same as or shorter than the total exposure time during a direct emigration (Appendix). In fact the two would be the same only in the highly theoretical case when all items are transported simultaneously. By contrast, in reality, with only a proportion of all transportable items being transported simultaneously, the smaller that proportion, the shorter is the total exposure time during staged emigration compared to direct emigration (Appendix).

Table 2. Number of colonies carrying out staged and direct emigrations to the good nest during binary choice experiments on nests of different quality

Experiment no.	Emigration type		Total
	Staged	Direct	
1	9	3	12 of 12 (all dynamics data colonies)
2	9	7	16 of 18 (colonies 13 & 14 N/A: late emigrations and little information on dynamics)
3	12	4	16 of 18 (colonies 2b & 5b chose P nest)
Total	30	14	44 of 48

G: good nest; P: poor nest.

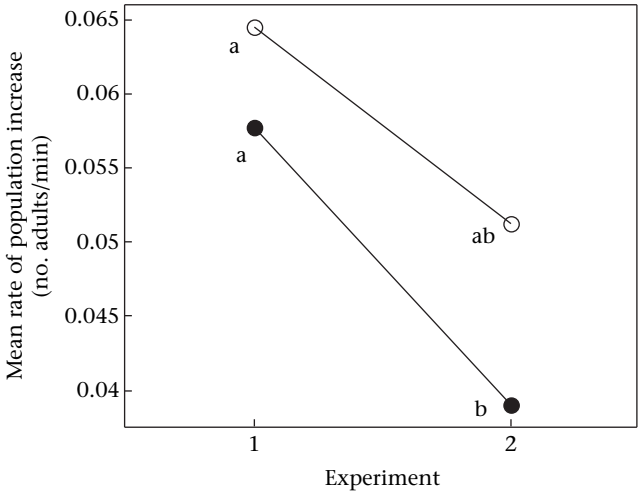
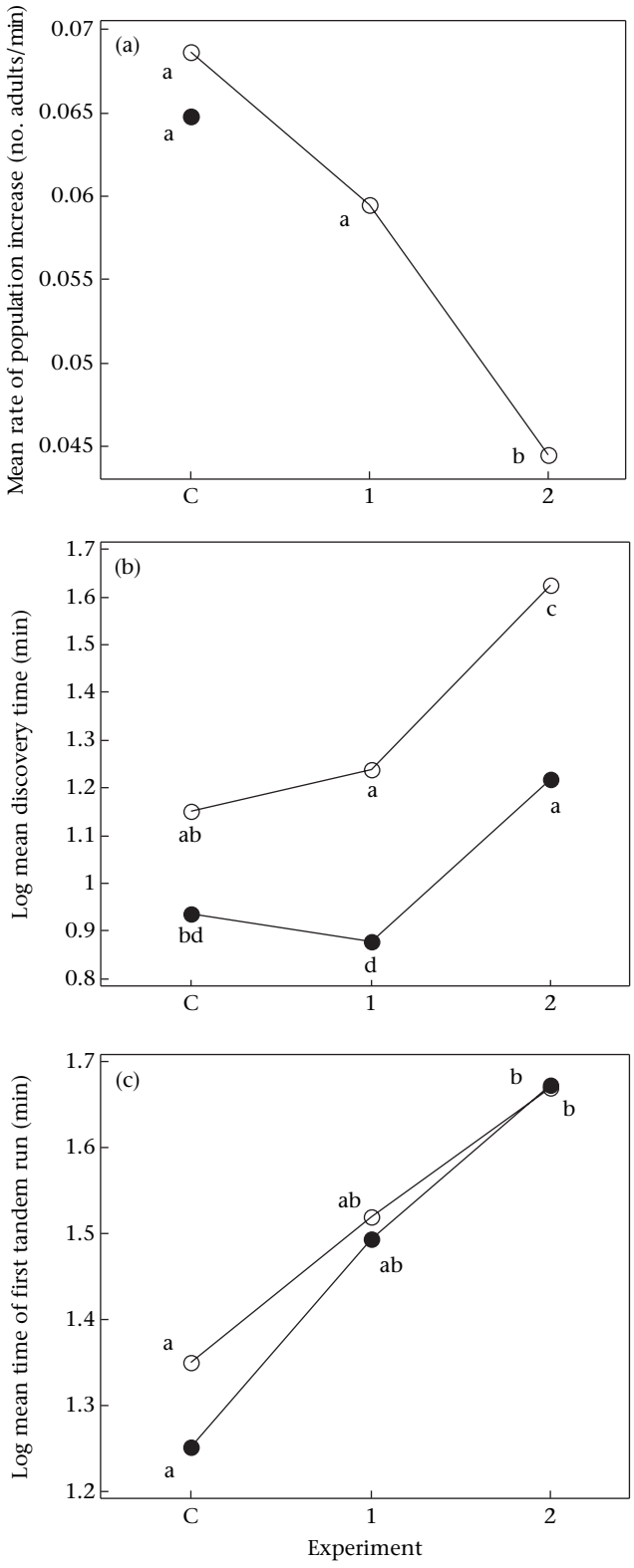


Figure 3. Mean rate of population increase (number of adults/min) in the good nest for staged and direct emigrations in experiment 1 (good nest at 60 cm from the old nest) and experiment 2 (good nest at 90 cm). In both experiments, the poor nest was at 30 cm. Different combinations of letters correspond to a significant difference in pairwise post hoc comparisons with a Tukey test at the 5% significance level. ○: Direct emigration; ●: staged emigration.



Influence of Nest Distance on Nest Choice

As might be expected, increasing distance to the good nest delayed all stages of the emigration to the good nest, but it also delayed all stages of the emigration to the poor nest which was always at 30 cm.

The rate of population increase in the good nest was affected significantly by the type of experiment ($F_{2,47} = 10.86$, $P < 0.001$; Fig. 4a). This was accounted for by the significantly slower mean rate of population increase in the good nest when it was at 90 cm (experiment 2) compared to when it was either at 60 cm in the absence of a poor alternative (Tukey test: experiment C: $T = -4.301$, $P = 0.0005$) or at 60 cm in the presence of a poor alternative (experiment 1: $T = -2.663$, $P = 0.050$; Fig. 4a). There was no significant difference in the mean rate of population increase in the good nest when it was at 60 cm whether the poor nest was present or absent (experiment 1 versus experiment C: $T = -1.532$, $P = 0.427$; Fig. 4a). In the control (experiment C), the rate of population increase in the good nest was not significantly different from the rate of population increase in the poor nest (GLM with factor nest type nested within factor experiment: $F_{1,47} = 0.39$, $P = 0.537$; experiment C; Fig. 4a).

Discovery time was affected significantly by the type of experiment (GLM: $F_{2,60} = 32.21$, $P < 0.001$) and the type of nest ($F_{1,60} = 62.40$, $P < 0.001$) but there was no significant interaction between the two ($F_{2,60} = 1.88$, $P = 0.162$; Fig. 4b). The good nest was discovered significantly later when it was at 90 cm (experiment 2) than when it was either at 60 cm in the absence of a poor alternative (Tukey test: experiment C: $T = 6.564$, $P < 0.0001$) or at 60 cm in the presence of a poor alternative (experiment 1: $T = 5.370$, $P < 0.0001$; Fig. 4b). There was no significant difference in the mean discovery time of the good nest when it was at 60 cm whether the poor nest was present or absent (experiment 1 versus C: $T = 1.143$, $P = 0.861$; Fig. 4b). The pattern with the poor nest was exactly the same. It was discovered significantly later when the good nest was at 90 cm (experiment 2) than when it was absent (experiment C: $T = 3.831$, $P = 0.004$) or when it was at 60 cm (experiment 1: $T = 4.746$, $P = 0.0002$; Fig. 4b). The discovery time of the poor nest when the good nest was at 60 cm was not significantly different from that when the good nest was absent (experiment 1 versus C: $T = -0.749$, $P = 0.975$; Fig. 4b). While there was no significant difference between the discovery times for the good and poor nests when they were presented independently

Figure 4. Descriptors of the dynamics of the emigration in experiment C (control: poor nest at 30 cm and good nest at 60 cm were presented separately), experiment 1 (poor nest at 30 cm and good nest at 60 cm were presented simultaneously) and experiment 2 (poor nest at 30 cm and good nest at 90 cm were presented simultaneously): (a) mean rate of population increase (number of adults/min), (b) log mean discovery time (min), and (c) log mean time of first tandem run (min). Different combinations of letters correspond to a significant difference in pairwise post hoc comparisons with a Tukey test at the 5% significance level. ○: Good nest; ●: poor nest.

(experiment C: $T = -2.795$, $P = 0.072$), the discovery time for the good nest was significantly longer when the good and poor nests were presented simultaneously (experiment 1: $T = -4.782$, $P = 0.0002$; experiment 2: $T = -6.588$, $P < 0.0001$; Fig. 4b).

Once the discovery time had been taken into account, the time of the first tandem run was affected significantly by the type of experiment (GLM: $F_{2,63} = 16.87$, $P < 0.001$) but not by the type of nest ($F_{1,63} = 0.59$, $P = 0.446$) and there was no significant interaction between the two ($F_{2,63} = 0.32$, $P = 0.724$; Fig. 4c). The first tandem run to the good nest occurred significantly later when it was at 90 cm (experiment 2) than when it was at 60 cm in the absence of a poor alternative (Tukey test: experiment C: $T = 3.620$, $P = 0.007$) but not when it was at 60 cm in the presence of a poor alternative (experiment 1: $T = 1.752$, $P = 0.504$; Fig. 4c). There was no significant difference in the mean time of the first tandem run to the good nest when it was at 60 cm whether the poor nest was present or absent (experiment 1 versus C: $T = 1.791$, $P = 0.479$; Fig. 4c). The pattern with the poor nest was exactly the same. The first tandem run to it occurred significantly later when the good nest was at 90 cm (experiment 2) than when it was absent (experiment C: $T = 4.563$, $P = 0.0003$) but not when it was at 60 cm (experiment 1: $T = 1.998$, $P = 0.355$; Fig. 4c). The time of the first tandem run to the poor nest when the good nest was at 60 cm was not significantly different from that when the good nest was absent (experiment 1 versus C: $T = 2.443$, $P = 0.158$; Fig. 4c).

Once discovery times and times to first tandem runs were taken into account, there were no significant differences in the times to first carrying in the comparisons between all treatments and the control.

DISCUSSION

In all of the experiments, in which a good nest was more distant than a collinear poor one, the ants were able overwhelmingly to choose and occupy the good one exclusively. Such was the case even when the good nest was more than nine times further away than the poor one (experiment 3). Moreover, this was not due to the ants first completely occupying the nearby poor nest and then secondarily emigrating to the better one. These ants can move up the property ladder (Dornhaus et al. 2004), but in earlier work on such 'moving to improve' the ants were fully established in one nest before moving to a better one. Here, for the most part, the ants either emigrated directly to the better nest, or simultaneously emigrated to the poor one and the good one and later seamlessly redirected all of their nestmates to the distant and better nest. Indeed, two-thirds of all the emigrations we observed were staged through the poor nest (Table 2).

Our analysis of the dynamics shows that direct emigrations to the good nest proceeded at a higher rate than staged emigrations, that is, emigrations that involved the poor nest as a stepping stone (Figs 2, 3). However, staged emigrations may minimize exposure of the brood and other passive colony members because these can be rapidly rehoused in the nearby poor nest before being swiftly moved on to the better one (Appendix).

How can these ants choose a distant good nest in preference to a poor one that is not only much nearer but is also directly in the emigration path to the better one? It is clear that greater emigration distances are costly in terms of rates of nest occupancy (Fig. 4a) and nests at greater distances take more time to discover (Fig. 4b). So choosing between a distant good nest or a nearby poor one would seem problematic.

There are three ways in which the ants might minimize their risk of being trapped by a nearby but low-quality nest site so that they can benefit from a better but more distant one. First, they might hesitate less over distant nests of high quality or hesitate longer over poor nearby nests. The latter seems both simpler and more parsimonious. It has already been established that these ants learn about and then discriminate against low-quality nearby nests (Franks et al. 2007b) possibly to focus their search efforts elsewhere for higher-quality nests. Second, they may vary the quorum threshold with distance to discriminate against poor-quality nearby nests. We know that these ants can use flexible quorum thresholds (Franks et al. 2003a; Dornhaus et al. 2004). Third, these ants might continue to search for alternatives, that is, have the potential to switch preference, if they have only encountered a low-quality nest. Franks et al. (2007c) showed that such switching by scouts is so powerful that these ants can redirect their emigration to a belatedly discovered better nest even when carrying has begun to one of lower quality. In the experiments by Franks et al. (2007c), a small arena was used and the better nest was introduced to the arena only after carrying had begun to an initially present (mediocre) nest. The mediocre nest and the belatedly introduced better one were equidistant from the original nest. Such experiments, with belatedly introduced better nests, suggest that scouts may continue to search for better alternatives even after carrying has begun. The experiments reported here suggest that such 'switching' may also occur at any time during the decision-making process, that is, even before the start of carrying. We are currently conducting experiments with individually marked workers to test this prediction.

Moreover, in the experiments reported in this paper, the time between the discovery of a nest and the first tandem run to it is likely to have been important for nest selection. Indeed, first carrying times, once discovery times and times to first tandem runs had been subtracted, showed no significant differences for all comparisons between any of the nests in the control and experiments 1 and 2. This strongly suggests that in these experiments, the first carrying events occurred after all the major choices had been made. In other words, to begin to understand the extraordinary ability of the ants to choose a better but much more distant nest we need to focus on times to first tandem runs (Fig. 4c).

For all of the within-treatment comparisons of the time lags between first discovery and first tandem runs there were no significant differences (i.e. for the comparison of the control with a single poor nest at 30 cm and a single good one at 60 cm, or for either the two concurrently

available nests in experiment 1 or those within experiment 2). Moreover, the trend lines in Fig. 4c are effectively parallel and there are no significant interactions between the variables. The time delays before the first tandem runs were longer, albeit not significantly so, in experiment 1 than in the control even though the same arenas were used so that search areas and distances to the nests were identical. Although we emphasize that certain of the time differences are not significant, the general trend seen in Fig. 4c (which clearly continues into the comparison with the results for experiment 2) does suggest that the significant differences between the results in the control and experiment 2 might be caused by interference between the two nests that may have occurred in experiment 2 but could not have occurred in the control.

The 'trend' to increasing delay between first discovery and first tandem run to the good nest in the progressive comparison from control to experiment 1 to experiment 2 may be explained by the increasing difficulty of the task. The poor nest was present in experiment 1, but not in the control, and may have interfered in some way and the good nest was further away in experiment 2 than in experiment 1.

The almost identical 'trend' to increasing delay between first discovery and first tandem run to the poor nest (from the control to experiment 1 to experiment 2) may also be explained by the increasing difficulty of the task. The good nest was present in experiment 1 (but not in the control) and might have been a source of interference. Moreover, the arena was larger, and hence opportunities to become lost were more plentiful, in experiment 2 versus experiment 1 or the control.

Nevertheless, it seems surprising that the tandem times to the poor nest were progressively so much longer from the control to experiment 1 to experiment 2. Tandem runs are rather straight and seem to begin only when the first leader has found an effective route (Franks & Richardson 2006). So area effects associated with the change in arenas, between experiment 2 and both the control and experiment 1, should not be a major factor and crucially the distance to the poor nest was constant throughout.

So it seems that if tandem running to the distant good nest is more difficult, this causes more difficulty in tandem running to the poor nest. This might be associated with potential tandem recruiters, to the poor nest, possibly switching to the alternative better nest which is further away. Such switching might cause the pool of potential tandem runners to the poor nest to be increasingly 'diluted' by an increase in the distance to the good nest. So we hypothesize that the nests can 'interfere' with recruitment to one another and this interference can grow with the increasingly difficult task of finding a better but more distant alternative. Continuing switching and dilution of the pool of active ants may all play a role in this.

These ants may be able actively to compensate for distances travelled so that nearby poor nests are not chosen over better but more distant ones. This could occur if the ants increase recruitment hesitation times to compensate in part for shorter travel times to nearby nests of low quality. This is potentially plausible given that ants can estimate distances with remarkable accuracy (Wittlinger et al. 2006). However, Planqué et al. (2007a) have investigated with a mathematical model the potential roles of hesitation to recruit versus switching in nest choice and it appears that, in cases such as those investigated here, switching is a much more powerful mechanism to favour better nests than hesitating for longer over poor ones (R. Planqué, personal communication).

Our results clearly show that ants are able to choose on the basis of quality rather than distance even though they can use a nearby nest as a stepping stone to a better but more distant alternative to minimize exposure of the brood. Franks et al. (2007b) showed that these ants can latently learn about nearby poor-quality nests when they have no need to emigrate and use this information when they do need to emigrate to focus their search for something better elsewhere. So this result, together with the ones reported here and others (Dornhaus et al. 2004; Franks et al. 2007c), certainly suggests that these ants will favour high-quality nests, even at the costs of longer emigrations, over the short-term convenience of proximate mediocrity.

One of the reasons that ants need such sophisticated decision-making systems to choose new nests is that potential nest sites provide only local cues to their quality. By contrast, in mating systems males should provide honest signals which they may broadcast over considerable distances to choosy females. Thus a female searching for a high-quality calling male, but finding a poorer one in the way, may use, for example, the lower pitch of a bigger and better, but more distant, male's call to avoid being trapped by the weaker call of a poorer but nearer suitor (Greenfield & Rand 2000; Hutchinson 2005). Many high-quality males also time their calls to precede or follow those of inferior males (Snedden & Greenfield 1998; Berg & Greenfield 2005). In such situations, both females and better males should gain from signalling systems that avoid distance effects (Gerhardt 1994; Snedden et al. 1998; Gerhardt et al. 2007).

Social insect colonies seeking new homes face a very different problem. They have to gather actively all of the information they need by inspecting and evaluating both near and distant new nest sites. One huge advantage for social insect colonies, however, is that different members of the same society can search simultaneously in different places; some may continue searching for something better even after they have personally initiated an emigration to a conveniently close but mediocre alternative.

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Appendix

Comparison between the total exposure times for staged and direct emigrations

Consider that:

N is number of items to be transported

n is number of items transported simultaneously

$$\beta = \frac{N}{n}$$

d_{OP} is distance between Old Nest (ON) and Poor Nest (PN)

d_{PG} is distance between Poor Nest (PN) and Good Nest (GN)

d_{OG} is distance between Old Nest (ON) and Good Nest (GN), $d_{OG} = d_{OP} + d_{PG}$

α is transport speed

T_{SE} is total exposure time for transported items during Staged Emigration (SE)

T_{DE} is total exposure time for transported items during Direct Emigration (DE)

T_1 is exposure time for leg from ON to PN in SE

T_2 is exposure time for leg from PN to GN in SE

The sum of an arithmetic progression $a_1 + a_2 + \cdots + a_n$ with n terms and common difference d between successive terms is:

$$S = n\frac{(a_1 + a_n)}{2}$$

Result

After appropriate algebraic calculations for T_{SE} and T_{DE}, using the above notations, the result is that:

$$\frac{T_{SE}}{T_{DE}} = \frac{d_{OP} + d_{PG}\frac{n}{N}}{d_{OP} + d_{PG}}$$

This shows that T_{SE} can only be the same or shorter than T_{DE} because $\frac{n}{N}$ can only be equal to or less than 1. $\frac{n}{N}$ cannot be greater than 1 because n (number of items transported simultaneously) cannot be greater than N (number of items to be transported).

T_{SE} is the same as T_{DE} when $n = N$. The smaller the number of items transported simultaneously, n, the shorter is T_{SE} compared to T_{DE}.

Details of the calculation

The exposure time during the first leg of the journey in a SE, i.e. between the ON and the PN, is the sum of the exposures of all items (both those that are transported and those still remaining at the old nest) during forward and return journeys. For example, during the first forward journey from the ON to the PN, the exposure time is equal to the total number of items, N, multiplied by the time each item is exposed: in this case the distance between the ON and the PN, d_{OP}, divided by the transport speed, α. The calculation for the exposure time during the first return journey follows exactly the same logic but in this case the total number of items, N, has been reduced by the number, n, of items that have already been transported to the safety of the PN. Then follows the next forward journey with $(N - n)$ exposed items and so on and so forth. Therefore,

$$\begin{aligned} T_1 = {} & N\frac{d_{OP}}{\alpha} + (N-n)\frac{d_{OP}}{\alpha} + (N-n)\frac{d_{OP}}{\alpha} \\ & + (N-2n)\frac{d_{OP}}{\alpha} + (N-2n)\frac{d_{OP}}{\alpha} \\ & + (N-3n)\frac{d_{OP}}{\alpha} + \cdots + [N-(\beta-1)n]\frac{d_{OP}}{\alpha} \\ & + [N-(\beta-1)n]\frac{d_{OP}}{\alpha}, \end{aligned} \tag{A1}$$

where the first term, last term and all intermediate odd-number terms represent exposure times for the forward journey while the second, penultimate and all intermediate even-number terms represent exposure times for the return journey.

Equation (A1) could be regarded as the sum of two arithmetic progressions: one for the exposure times of the forward journeys and one for the exposure times of the return journeys. In each case the common difference d between successive terms is $d = n\frac{d_{OP}}{\alpha}$.

The sum for the forward journeys is:

$$S_F = \frac{\beta\left\langle N\frac{d_{OP}}{\alpha} + [N-(\beta-1)n]\frac{d_{OP}}{\alpha}\right\rangle}{2} \tag{A2}$$

The sum for the return journeys is:

$$S_R = \frac{(\beta-1)\left\langle (N-n)\frac{d_{OP}}{\alpha} + [N-(\beta-1)n]\frac{d_{OP}}{\alpha}\right\rangle}{2} \tag{A3}$$

Therefore,

$$\begin{aligned} T_1 = S_F + S_R &= \beta\frac{d_{OP}}{2\alpha}\Big[(2N-(\beta-1)n\Big] \\ &\quad + (\beta-1)\frac{d_{OP}}{2\alpha}\Big[(2N-n-(\beta-1)n\Big] \\ &= \beta\frac{d_{OP}}{2\alpha}(2N-\beta n+n) \\ &\quad + (\beta-1)\frac{d_{OP}}{2\alpha}(2N-n-\beta n+n) \\ &= \frac{d_{OP}}{2\alpha}(2\beta N-\beta^2 n+\beta n+2\beta N-\beta^2 n-2N+\beta n) \\ &= \frac{d_{OP}}{2\alpha}(4\beta N-2\beta^2 n+2\beta n-2N) \\ &= \frac{d_{OP}}{2\alpha}2(2\beta N-\beta^2 n+\beta n-N) \\ &= \frac{d_{OP}}{\alpha}(2\beta N-\beta^2 n+\beta n-N) \\ &= \frac{d_{OP}}{\alpha}\Big[N(2\beta-1)-\beta n(\beta-1)\Big] \end{aligned} \tag{A4}$$

Since $\beta = \frac{N}{n}$, equation (A4) becomes:

$$\begin{aligned} T_1 &= \frac{d_{OP}}{\alpha}\left[N\left(2\frac{N}{n}-1\right) - \frac{N}{n}n\left(\frac{N}{n}-1\right)\right] \\ &= \frac{d_{OP}}{\alpha}\left[N\left(2\frac{N}{n}-1-\frac{N}{n}+1\right)\right] \\ &= \frac{d_{OP}}{\alpha}N\frac{N}{n} \\ &= \frac{d_{OP}}{\alpha}\frac{N^2}{n} \end{aligned} \tag{A5}$$

The exposure time during the second leg of the journey in a SE, i.e. between the PN and the GN, is the sum of the exposures of the transported items only, all of which are moved from the safety of the PN to the safety of the GN. Therefore, exposure time involves only forward journeys and is the simple multiple of all the items, N, and the time it takes to transport an item from the PN to the GN, in this case the distance between the PN and the GN, d_{PG}, divided by the transport speed, α. Therefore,

$$T_2 = N\frac{d_{PG}}{\alpha} \tag{A6}$$

Therefore,

$$T_{SE} = T_1 + T_2 = \frac{d_{OP}}{\alpha}\frac{N^2}{n} + N\frac{d_{PG}}{\alpha} \tag{A7}$$

The calculation of the exposure time during the single leg of the journey in a DE, i.e. between the ON and the GN, follows exactly the same logic as the calculation of the exposure time for the first leg, T_1, of the journey in a SE. The only difference is that the distance has to be between the ON and the GN, i.e. d_{OG} rather than the distance between the ON and the PN, i.e. d_{OP}. Therefore,

$$T_{DE} = \frac{d_{OG}}{\alpha}\frac{N^2}{n} \tag{A8}$$

Therefore, the ratio between the total exposure times for SE and DE is:

$$\begin{aligned}\frac{T_{SE}}{T_{DE}} &= \frac{d_{OP}}{\alpha}\frac{\alpha}{d_{OG}}\frac{N^2}{n}\frac{n}{N^2} + \frac{d_{PG}}{\alpha}\frac{\alpha}{d_{OG}}N\frac{n}{N^2} \\ &= \frac{d_{OP}}{d_{OG}} + \frac{d_{PG}}{d_{OG}}\frac{nN}{N^2} \\ &= \frac{d_{OP}}{d_{OG}} + \frac{d_{PG}}{d_{OG}}\frac{n}{N}\end{aligned} \tag{A9}$$

Since $d_{OG} = d_{OP} + d_{PG}$,

$$\begin{aligned}\frac{T_{SE}}{T_{DE}} &= \frac{d_{OP}}{(d_{OP} + d_{PG})} + \frac{d_{PG}}{(d_{OP} + d_{PG})}\frac{n}{N} \\ &= \frac{d_{OP} + d_{PG}\frac{n}{N}}{d_{OP} + d_{PG}}\end{aligned} \tag{A10}$$