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Polydomy enhances foraging performance in ant colonies

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Collective foraging confers benefits in terms of reduced predation risk and access to social information, but it heightens local competition when resources are limited. In social insects, resource limitation has been suggested as a possible cause for the typical decrease in *per capita* productivity observed with increasing colony size, a phenomenon known as Michener's paradox. Polydomy (distribution of a colony's brood and workers across multiple nests) is believed to help circumvent this paradox through its positive effect on foraging efficiency, but there is still little supporting evidence for this hypothesis. Here, we show experimentally that polydomy enhances the foraging performance of food-deprived *Temnothorax nylanderi* ant colonies via several mechanisms. First, polydomy influences task allocation within colonies, resulting in faster retrieval of protein resources. Second, communication between sister nests reduces search times for far away resources. Third, colonies move queens, brood and workers across available nest sites in response to spatial heterogeneities in protein and carbohydrate resources. This suggests that polydomy represents a flexible mechanism for space occupancy, helping ant colonies adjust to the environment.

1. Background

Many animals gather food collectively [1,2]. Collective foraging can confer important benefits, including decreased predation risk [3], increased ability to capture, monopolize and/or defend resources [4–6], and decreased search times through the use of social information [4,7,8]. However, collective foraging may also incur costs [1]. For example, local competition may decrease individual feeding rates [4,9,10]. In addition, groups deplete limited resources more rapidly and need to look for new resources more frequently than solitary foragers [11]. These costs are particularly significant for central-place foragers, which must return to their home site between foraging bouts and cannot move to a new territory when their foraging range has been depleted [12].

Social insects are ideal model systems to study the costs and benefits associated with collective central-place foraging. In social insects, larger colonies typically experience lower variability in foraging success [13], higher probability of survival [14], more efficient defence against predators and parasites [15], and enhanced exploitative and competitive abilities while foraging [16]. However, there are also costs associated with large colony size: many social insects experience a decrease in *per-capita* productivity with increasing colony size, a phenomenon known as 'Michener's paradox' [11,17,18]. One possible cause for Michener's paradox is a decrease in *per-capita* foraging success as the number of foragers increases within a finite territory, resulting in faster resource depletion [11]. Michener's paradox may also result from population-dependent changes in the division of labour, such as an increase in the proportion of inactive workers in growing colonies [19,20]. In ants, polydomy has been suggested to allow colonies to overcome these constraints while maintaining the benefits associated with a large colony size [19,20]. Polydomy is a form of social organization in which a single colony occupies multiple physically distinct, but socially interconnected nests, each containing brood, workers and potentially a queen [20,21]. The

ultimate and proximate causes of polydomy are still highly debated [20,21]. However, polydomy has been suggested to help preserve efficient organization of labour by reducing population size in individual nests [19,20]. In addition, polydomy is generally believed to help colonies overcome territory saturation by allowing them to carry out 'dispersed central-place foraging' [20–25], that is, harvest resources from multiple nest entrances spread over the foraging area. Dispersed central-place foraging is believed to enhance foraging through a variety of mechanisms. First, it is expected to reduce food search costs by increasing the total searched area while decreasing the overlap between foragers' search paths [5,6,25–30]. Second, dispersed central-place foraging should decrease food transport costs by reducing the average distance between food sources and the nearest nest entrance [6,23,24,28,31–40]. Third, foraging over a larger territory is considered beneficial by allowing colonies to diversify their food sources [20,21]. Fourth, inter-nest recruitment to food sources and/or food redistribution between nests is expected to reduce the variance in the colony's foraging success over time [24,25,27,35,36,38–44]. Though the potential advantages of polydomy have been repeatedly mentioned in the literature, they are supported by surprisingly little experimental evidence. The influence of polydomy on task allocation has never been formally investigated. Similarly, most support for the foraging benefits of dispersed central-place foraging derives from models [25,27,34] and observations that polydomous colonies establish new nests near stable food sources [22–24,33,36,38–40]. Few studies have attempted to quantify the foraging efficiency of polydomous ant colonies [5,6,24,26,38,45], and even fewer used experimental manipulations to evaluate the effect of nest number on foraging efficiency [5,45].

Here, we experimentally investigate the relationship between polydomy and foraging in the ant *Temnothorax nylander* in conditions of hunger relief. *T. nylander* ants form small colonies (10–250 workers) with a single, singly mated queen. In this species, as in other species of the genus *Temnothorax*, foragers are mostly opportunistic and exploit a mixture of ephemeral (dead and live arthropods, plant material [46]) and more durable food sources (harvesting sweet secretions from galls [46] and aphids [47–49], hunting patches of aggregated springtails [50–53]). Workers forage mainly solitarily, but when they encounter sizeable food items or large food patches, foragers recruit nestmates via 'tandem runs', in which the informed worker physically leads the follower to the food [46,54]. Colonies inhabit natural cavities such as hollow acorns or rotten twigs and display a typical seasonal polydomy cycle: colonies are spread across multiple nests in spring and summer, and coalesce into a single nest in autumn for overwintering [21]. We focused on the polydomous phase to investigate (i) the relationship between polydomy, task allocation and foraging activity; (ii) the effect of communication between polydomous nests on food search time; and (iii) whether the need for diet diversification can trigger the foundation of new polydomous nests.

2. Material and methods

(a) Collection and rearing of colonies

Temnothorax nylander colonies were collected in Forêt de Dorigny, Lausanne, Switzerland, in spring 2014 and 2015. Colonies were maintained under controlled laboratory conditions (14 L:10 D

cycle, 25°C, 55% RH) and housed in nests made of a cardboard perimeter sandwiched between two glass slides, delimiting a rectangular nest cavity of $36 \times 48 \times 1$ mm with an entrance of 8×2 mm. They were kept in $155 \times 135 \times 50$ mm plastic boxes with Fluon-coated walls to prevent the ants from escaping. Colonies were fed weekly with an artificial diet, 10% honey solution and *ad libitum* water.

(b) General experimental procedures

To ensure that foraging motivation was comparable across colonies and treatments, each colony was given fresh food and allowed to forage freely for 24 h, then kept without food for exactly 7 days before being used in an experiment. In all experiments, colonies were then moved into experimental nests (see below) and allowed to acclimatize to these nests for 24 h before being transferred to the experimental arena (see below). Colonies were then left to explore the arena freely for another 24 h before any food was provided. Colonies were therefore deprived of food for a total of 9 days. This corresponds to moderate food deprivation for *Temnothorax* colonies, which can sustain starvation without increased mortality for two months, and survive in those conditions for up to eight months [55]. Previous studies of foraging in *Temnothorax* ants have used food deprivation periods of 14 days without detecting harmful effects [56–58].

Experimental arenas consisted of a large central box ($155 \times 135 \times 50$ mm) connected via tubes (diameter 0.5 cm, length 10 cm in experiment 1; diameter 0.8 cm, length 14 cm in experiments 2 and 3) to two smaller peripheral boxes ($100 \times 88 \times 40$ mm). The total length of the arena (less than 40 cm) was therefore well within the typical foraging range of *Temnothorax* colonies in the field (1–2 m [51]). Throughout experiments, water was provided in cotton-stoppered 1.5 ml Eppendorf tubes. Water tubes were positioned on top of each experimental nest, in order to avoid spatial biases due to water collection.

Temnothorax colonies have been shown to naturally allocate an area of approximately 5 mm^2 per adult ant when building their nest walls freely [59]. This corresponds to an area range of $3.5\text{--}4.9 \text{ cm}^2$ for the colonies used in experiments 1 and 2 ($n = 16$; queen, brood and 69–97 workers). In these experiments, we therefore used standardized experimental nests consisting of either a single 4 cm^2 chamber (monodomous treatments), or two fully separated, identical 2 cm^2 chambers across which colonies split themselves (polydomous treatments). Visual checks indicated that the distribution of workers and brood was even between the polydomous nest chambers. In experiment 3, the variation in colony size was much greater ($n = 24$; queen, brood and 84–250 workers), so we used tailor-made polydomous nests consisting of two chambers, each of area $A = N \times 2.5 \text{ mm}^2$, where N is the number of adults in each colony.

In all experiments, all colonies experienced all treatments in a pseudorandom order: for example, in experiment 1, half of the colonies experienced the monodomous treatment first, whereas the other half experienced the polydomous treatment first. Experiments were carried out in successive replicates in which the same number of colonies were allocated to each treatment. Colonies were given at least one week rest between successive replicates in order to minimize possible learning biases [60].

(c) Experiment 1: polydomy, task allocation and foraging output

In experiment 1, we tested whether polydomous and monodomous colonies differ in their foraging output through differences in task allocation, independently of the dispersion of nest entrances. We used experimental nests with the same total internal area and with two nest entrances positioned at the same locations, organized in either a single large chamber

(monodomous treatment) or two identical smaller chambers (polydomous treatment; figure 1a). Fourteen colonies housed in experimental nests were placed in the middle of the central box, so that their nest entrances were at the same distance from the tubes leading to the peripheral boxes (figure 1a). After 24 h, a dish containing 10% honey solution was introduced into one of the two peripheral boxes, and a dish containing 10 *Drosophila melanogaster* flies was simultaneously introduced into the other one. The locations of the fly- and honey-peripheral boxes relative to the experimental room were alternated between colonies to minimize the possible effect of inherent spatial biases. Cameras controlled by software PSRemote (Breeze Systems) recorded a picture of each peripheral and central box once per hour during 1 day after food introduction. From these pictures, we determined for each time point: (i) the number of outside-nest workers within each box and (ii) the number of flies remaining intact (i.e. uneaten) in the fly-peripheral box. Picture analysis was performed using a blind procedure, that is, the experimenter was not aware of treatment at the time of picture analysis.

(d) Experiment 2: polydomy and food search time

In experiment 2, we investigated whether communication between polydomous nests contributes to decrease search times for unknown food sources. Fourteen colonies were moved into experimental nests consisting of two identical, fully disconnected chambers that were either adjacent ('clustered' treatment) or spatially separated ('dispersed' treatment, figure 1b; note that colonies were polydomous in both treatments). In the 'clustered' treatment, the two adjacent nests were placed into one of the two peripheral boxes, so that their respective entrances were at the same distance from the tube leading to the central box. In the 'dispersed' treatment, one nest (distant nest) was placed in one of the peripheral boxes in the same position as in the 'clustered' treatment, and the other (close nest) was placed in the middle of the central box (figure 1b). After 24 h, a dish containing a water solution of 10% honey and 20% blue food colouring (Happy Décor, Migros) was placed in the middle of the peripheral box opposite to the one containing the nest(s). Preliminary tests revealed that both foragers and trophallaxis receivers develop a visible blue coloration within minutes of first contact with the blue-coloured honey solution (electronic supplementary material, figure S1), allowing easy visual monitoring of access to food. We tested two predictions. First, the close nest in the 'dispersed' treatment should have access to food earlier than any other nest, because it is physically closer to the food source and separated from it via fewer tubes. Second, recruitment and/or food exchange between polydomous nests should result in the distant nest in the 'dispersed' treatment having access to food earlier than either nest in the 'clustered' treatment, even though they are at exactly the same distance from the food. To test these predictions, each nest was visually checked every 30 min for 6 h following food introduction, and we recorded the time at which blue-coloured ants were first observed inside. It should be noted that data recording was not performed blind to treatment in that experiment, which could potentially lead to inflated effect sizes.

(e) Experiment 3: polydomy and diet diversification

In experiment 3, we investigated whether colonies might become polydomous in order to improve their access to diversified food sources. Twenty-four colonies housed in single-chamber nests were placed in the middle of the central box. After 24 h, a carbohydrate source (10% honey solution) was introduced into one of the two peripheral boxes, and a protein source (flies) was introduced into the other peripheral box. The locations of the fly- and honey-peripheral boxes relative to the experimental room were alternated between colonies to minimize the possible effect of

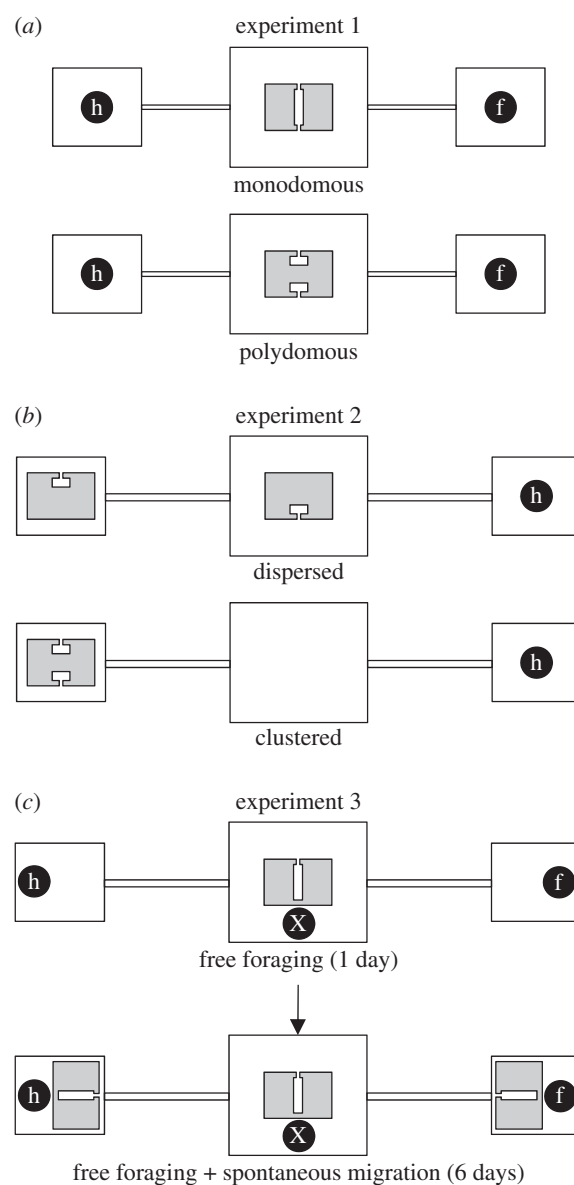


Figure 1. Top view of the experimental set-ups. (a) Experiment 1. Colonies housed in either a single-chamber nest (monodomous treatment) or a double-chamber nest (polydomous treatment) were placed in the middle of the central box. Twenty-four hours later, dishes containing either 10% honey solution (h) or 10 flies (f) were introduced into the peripheral boxes and foraging effort was measured hourly for an additional 24 h. (b) Experiment 2. Nests consisted of two disconnected chambers that were either distant from one another (dispersed treatment) or adjacent (clustered treatment). In the dispersed treatment, one nest was placed in one of the peripheral boxes and the other in the central box, whereas in the clustered treatment, both nest chambers were inside one of the peripheral boxes. Twenty-four hours later, a dish containing a blue honey solution (h) was placed into the peripheral box opposite to the nest(s). Nests were checked for the presence of blue-coloured ants every half hour for 6 h after food introduction. (c) Experiment 3. Colonies housed in a single-chamber nest were placed in the middle of the central box. Twenty-four hours later, a carbohydrate source (10% honey solution, 'h') was placed in one of the peripheral boxes, a protein source (flies, 'f') was placed in the opposite peripheral box, and a carbohydrate source only, a protein source only or both (treatments 'honey', 'fly' and 'honey and fly', respectively) were placed near the home nest inside the central box (position 'X'). Colonies were left to forage freely for 1 day; then two empty single-chamber nests were introduced into the peripheral boxes near the food sources. Colonies were left undisturbed for another 6 days, during which they had the opportunity to move spontaneously to one or both of the new nests.

inherent spatial biases. At the same time, we also introduced food next to the home nest in the central box (figure 1c). Treatments differed in the nature of the food introduced near the home nest: (i) a carbohydrate source only (10% honey solution; 'honey' treatment), (ii) a protein source only (*Drosophila*; 'fly' treatment) or (iii) both ('honey and fly' treatment). All food sources were replaced with fresh food every 24 h until the end of the experiment. One day after introducing the food, empty nest sites identical to the home nest were introduced into each peripheral box. We then recorded the number of workers, the presence/absence of brood and the presence/absence of the queen in each new nest every 24 h for the following 6 days. Data recording was performed after the old food trays had been removed and before the fresh food trays were reintroduced, so the observer was not aware of experimental treatments at the time of recording. Colonies were considered to have established an 'outstation' if there were workers but no brood inside a new nest [32,35,36], and they were considered to have established a polydomous nest if there were both workers and brood inside a new nest. We predicted that the lack of a fundamental dietary element (carbohydrates or proteins) near the home nest should increase the likelihood of colonies becoming polydomous in order to gain easier access to the complementary food source. The 'honey and fly' treatment was used as a control for the tendency of colonies to become polydomous under our experimental conditions, when there are no dietary limitations, and to determine their inherent preference for nests near either carbohydrate or protein food sources.

(f) Statistical analyses

All statistical analyses were performed using R v. 3.0.2. The number of flies consumed was compared between treatments using a Wilcoxon matched-pairs test. Temporal data were analysed by fitting mixed-effects Cox proportional hazard models using the R package 'coxme'. We used the R packages 'lmer' and 'lmerTest' to fit general linear mixed models (hereafter 'GLMM Normal') and generalized linear mixed models with Poisson distribution (count data; hereafter 'GLMM Poisson') or binomial distribution (binary data; hereafter 'GLMM Binomial'). All models were fitted using colony identity, replicate and, when relevant, nest location relative to the experimental room as random effects, and colony size as a fixed effect. For the GLMM Normal, data were transformed using the Yeo–Johnson power transformation [61], so the model's residuals were normally distributed (Shapiro–Wilk's test, $p = 0.41$). For the Cox models, the proportional hazards assumption was checked using the 'cox.zph' test from the R package 'survival'. This assumption was only violated by the variable 'colony size' in two models with 'time to polydomy' as dependent variable (experiment 3). Because its effect was not significant ($p > 0.19$), we removed that variable from these models. The proportional hazards assumption is thus verified in all Cox models presented below ($p > 0.3$ in all tests). Fixed effect significance was tested using two-tailed Satterthwaite's F -tests for the GLMM Normal, and two-tailed Wald χ^2 -tests otherwise. Whenever relevant, we used the R package 'multcomp' to correct for multiple comparisons using the Benjamini–Hochberg (BH) procedure [62]. In experiment 2, we used one-tailed post hoc tests as we had clear directional predictions on the order in which nests would get access to food.

3. Results

(a) Experiment 1: polydomy, task allocation and foraging output

The total number of workers observed outside the nest was significantly higher in polydomous than monodomous

conditions (figure 2a). This was mainly due to the number of workers in the peripheral box containing flies being higher in polydomous than monodomous conditions (figure 2b), whereas the number of workers in the peripheral box containing the honey solution and in the central box did not differ between treatments (figure 2c,d; GLMM Poisson, total: $\chi^2 = 10.99$, d.f. = 1, $p < 0.001$; fly box: $\chi^2 = 27.34$, d.f. = 1, $p < 0.0001$; honey box: $\chi^2 = 0.32$, d.f. = 1, $p = 0.57$; central box: $\chi^2 = 2.23$, d.f. = 1, $p = 0.14$). The difference in the number of workers in the fly box was not constant over time (interaction time \times treatment: $\chi^2 = 9.43$, d.f. = 1, $p < 0.005$), but was stronger during the first few hours following food introduction (figure 2a,b). This presumably corresponds to stronger recruitment to the fly source in polydomous conditions, which subsided after a few hours of food exploitation.

In agreement with these results, we found no differences between treatments in the total number of visits to the honey-peripheral box (figure 2e; GLMM Normal, $F_{1,12.39} = 0.12$, $p = 0.73$). By contrast, the rate of fly consumption was more than twice higher in polydomous than monodomous conditions (figure 2f, mixed-effect Cox model, $\chi^2 = 21.9$, d.f. = 1, $p < 0.0001$, hazard ratio (HR) = 2.7), though the total number of consumed flies after 24 h did not differ between treatments (Wilcoxon matched-pairs test, $V = 14.5$, $p = 0.37$).

(b) Experiment 2: polydomy and food search time

As predicted, the nest located close to the honey solution in the dispersed treatment got access to honey significantly earlier than all other nests (figure 3a; mixed-effect Cox model, nest effect: $\chi^2 = 30.84$, d.f. = 3, $p < 0.0001$; post hoc comparisons with BH correction, close versus distant: HR = 2.2, $z = 1.75$, $p = 0.04$; close versus first clustered nest: HR = 6.9, $z = 3.72$, $p < 0.0005$; close versus second clustered nest: HR = 25.5, $z = 5.2$, $p < 0.0001$). In addition, the distant nest in the dispersed treatment got access to food significantly earlier than either nest in the clustered treatment (figure 3a, distant versus first clustered nest: HR = 3.2, $z = 2.19$, $p = 0.017$; distant versus second clustered nest: HR = 11.66, $z = 4.08$, $p < 0.0001$), even though all three nests were located at the same distance from the honey solution (figure 1b). These results confirm that dispersed central-place foraging contributes to decrease food search time not only for nests that are close to the food source, but also for more distant nests, which presumably benefit from inter-nest communication (e.g. inter-nest recruitment to the food source or food exchange between nests).

The time between the first nest and the second nest getting access to food did not differ significantly between treatments (figure 3b, mixed-effect Cox model, $\chi^2 = 2.14$, d.f. = 1, $p = 0.14$). This suggests that once the first nest found the food, communication facilitated the second nest getting access to food to a similar extent in both treatments.

(c) Experiment 3: polydomy and diet diversification

Colonies quickly established outstations inside the empty nests that were offered to them: after 24 h, 76% of the new nests were occupied by workers, and after 6 days, more than 90% of colonies had at least one outstation. Neither the experimental treatment nor the food near the new nest (flies versus honey) had any effect on the time to establish an outstation (mixed-effect Cox model, treatment: $\chi^2 = 1.53$, d.f. = 2, $p = 0.46$; food: $\chi^2 = 1.57$, d.f. = 1, $p = 0.21$; interaction: $\chi^2 = 2.24$, d.f. = 2, $p = 0.33$). However, the number of workers in

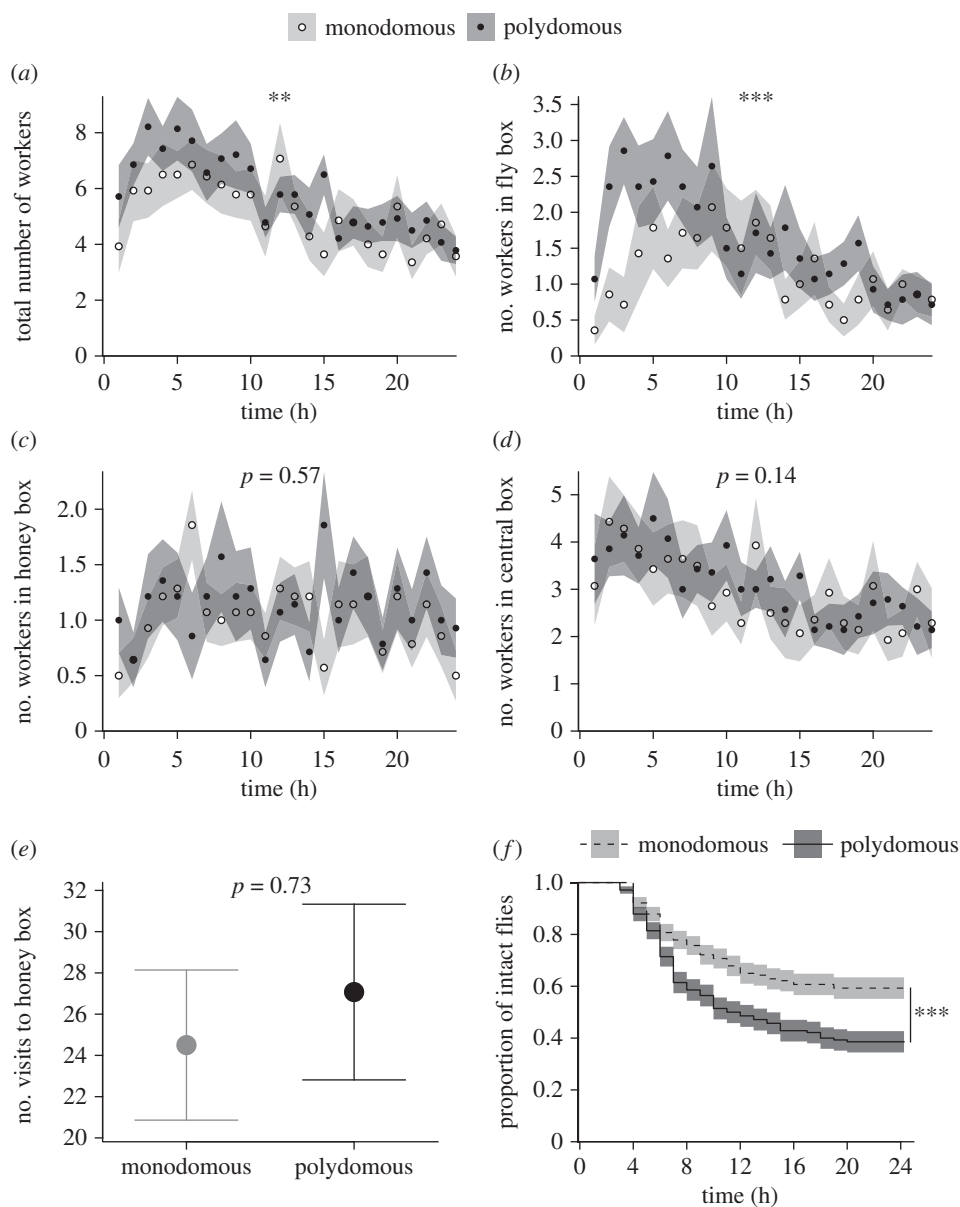


Figure 2. Experiment 1. (a–d) Number of outside-nest workers observed in the whole experimental arena (a), in the fly box (b), in the honey box (c) or in the central box (d) as a function of time since food was provided for monodominant (open circles, light grey shading) and polydominant (full circles, dark grey shading) treatments. Circles and shadings represent the mean \pm standard error, respectively. *** $p < 0.0001$; ** $p < 0.001$ (GLMM Poisson, effect of treatment). (e) Number of visits to the honey box recorded over the entire 24-h observation period for monodominant (light grey) and polydominant (dark grey) treatments. Points and whiskers represent the mean \pm standard error. The p -value is given for the effect of treatment on the number of visits (GLMM Normal). (f) Proportion of flies remaining intact as a function of time since flies were introduced for monodominant (dashed line, light grey shading) and polydominant (full line, dark grey shading) treatments. Lines and shadings represent the Kaplan–Meier estimates of the survival curves \pm standard errors, respectively. *** $p < 0.0001$ (mixed-effect Cox model, effect of treatment).

outstations depended significantly on food and its interaction with treatment (GLMM Poisson, food: $\chi^2 = 32.55$, d.f. = 1, $p < 0.0001$, treatment: $\chi^2 = 2.8$, d.f. = 2, $p < 0.25$, interaction: $\chi^2 = 27.78$, d.f. = 2, $p < 0.0001$; figure 4a). In both the control and the ‘honey’ treatment, there were significantly more workers in outstations near flies than in outstations near honey (post hoc comparisons with BH correction; control: $z = 5.45$, $p < 0.001$; ‘honey’ treatment: $z = 7.73$, $p < 0.01$), whereas colonies in the ‘fly’ treatment showed the opposite (non-significant) trend ($z = -1.94$, $p = 0.20$). Crucially, the degree of asymmetry in the occupancy of the two outstations differed significantly between all treatments (figure 4a). In the ‘honey’ treatment (i.e. when there was honey but no flies near the home nest), the preference for the fly outstation was significantly stronger than in the control, where both honey

and flies were available near the home nest ($z = -3$, $p = 0.013$). By contrast, in the ‘fly treatment’ (i.e. when there were flies but no honey near the home nest), worker distribution was significantly more biased towards the honey outstation than in both other treatments (‘fly’ versus control: $z = -5.30$, $p < 0.001$; ‘fly’ versus ‘honey’: $z = -7.36$, $p < 0.001$). Overall, these results show that the lack of a key element of the ants’ diet near the home nest (either proteins or carbohydrates) significantly affected the distribution of workers across outstations, showing a relative increase in the occupancy of the outstation near the missing food type.

Polydomy was much rarer than outstation establishment: after 6 days, less than 40% of the colonies had become polydomous (i.e. had moved brood into at least one new nest). We did not find a significant effect of treatment on the probability

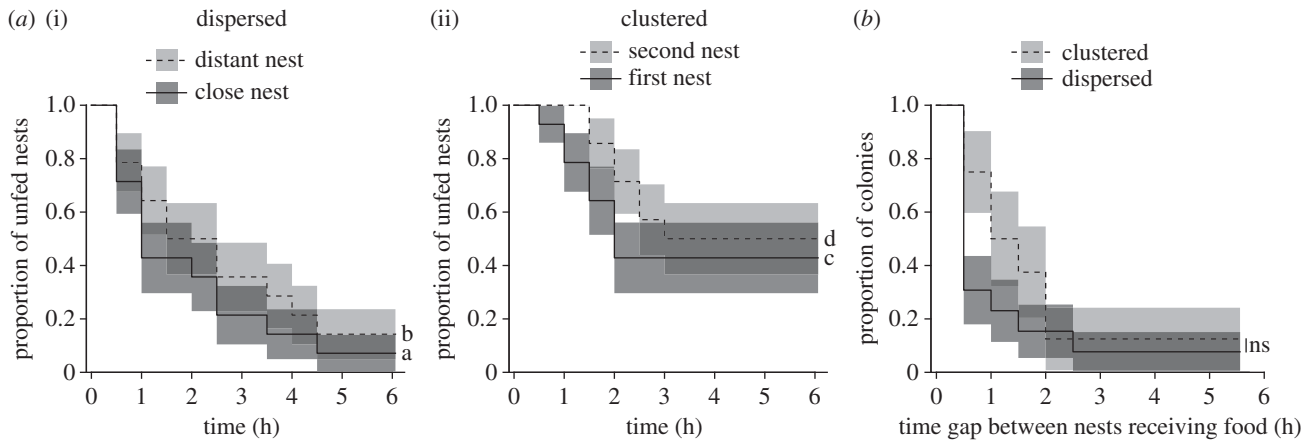


Figure 3. Experiment 2. (a) Survival curves of the time to receive food, showing the proportion of nests that have not received food yet as a function of time since food introduction (i): dispersed treatment; close nest: full line and dark grey shading; distant nest: dashed line and light grey shading; (ii): clustered treatment; first nest getting access to food: full line and dark grey shading; second nest: dashed line and light grey shading). (b) Survival curves of the time gap between the first and the second nest receiving food for the dispersed (full line, dark grey shading) and the clustered (dashed line, light grey shading) treatments. In both panels, lines and shadings represent the Kaplan–Meier estimates of the survival curves \pm standard errors, respectively. Different letters represent significant differences in post hoc comparisons ($p < 0.05$ after BH correction). n.s.: $p > 0.1$ (mixed-effect Cox model, effect of treatment).

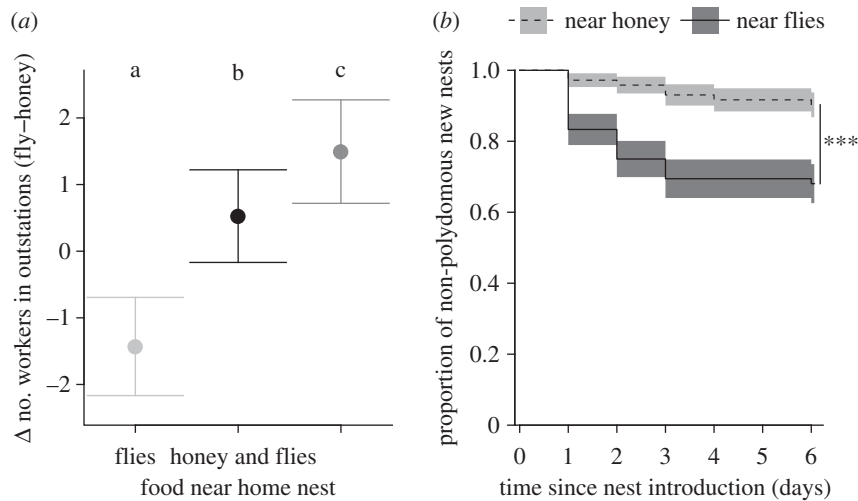


Figure 4. Experiment 3. (a) Number of workers in the fly outstation minus the number of workers in the honey outstation in different treatments. Statistical analysis was performed on the source data (i.e. on the number of workers per nest rather than on the difference between nests). Different letters represent significant differences in post hoc comparisons ($p < 0.05$ after BH correction). Note that this analysis was restricted to monodomous colonies that had not moved brood to a new nest site yet. (b) Proportion of non-polydomous new nests (i.e. new nest sites without brood) over time as a function of nearby food (honey: dashed line, light grey shading; flies: full line, dark grey shading). Each step in the survival curve corresponds to the foundation of one or several new polydomous nests, inhabited by both workers and brood. Statistical analysis revealed no effect of treatment and no interaction between food and treatment (mixed-effect Cox model, $p = 0.25$ and $p = 0.60$, respectively), so the plot represents the pooled data from all three treatments. *** $p < 0.0001$: mixed-effect Cox model, effect of food.

of colonies becoming polydomous (GLMM Binomial: $\chi^2 = 2.91$, d.f. = 2, $p = 0.23$), or on the time taken by colonies to become polydomous (mixed-effect Cox model: $\chi^2 = 2.97$, d.f. = 2, $p = 0.23$). However, colonies were significantly more likely to move brood and the queen to the new nest near flies (brood: 31.9% of cases; queen: 23.6%) than to the new nest near honey (brood: 9.7%; queen: 4.2%; GLMM Binomial, brood movement: $\chi^2 = 12.49$, d.f. = 1, $p < 0.0005$; queen movement: $\chi^2 = 10.10$, d.f. = 1, $p < 0.005$). Additionally, colonies that chose the fly-nest became polydomous significantly earlier than colonies that chose the honey-nest (figure 4b; mixed-effect Cox model: HR = 6.2, $\chi^2 = 17.72$, d.f. = 1, $p < 0.0001$). This preference for the fly-nest over the honey-nest was not affected by treatment (effect of treatment and interaction food \times treatment: $p \geq 0.25$ in all tests).

4. Discussion

In this study, we quantified the foraging performance of monodomous and polydomous colonies of the ant *T. nylanderii* using two measures: rate of food exploitation (experiment 1) and time to find an unknown food source (experiment 2). Both experiments supported the long-standing claim that polydomy enhances foraging, at least in conditions of hunger relief. Our findings are therefore consistent with the hypothesis that polydomy may help *Temnothorax* ants overcome Michener's paradox by increasing *per capita* foraging output when colonies are spread across multiple nests. In particular, we provide experimental evidence for two foraging-enhancing processes associated with division of labour and dispersion of nest entrances, respectively. First, colonies allocate more foragers to

protein collection in polydomous than monodomous conditions, resulting in a higher exploitation rate of protein sources (*Drosophila* flies in experiment 1). Crucially, the difference in the number of foragers gathering flies emerged even though colonies had similar dietary requirements in the two treatments: the 9-day food deprivation period ensured that hunger levels were comparable; our paired design ensured that the total numbers of queens, workers and brood items of each stage were the same for each colony; and the pseudorandom treatment ordering ensured that there was no systematic, seasonal difference in protein requirement. Additionally, the total nesting area and the number and location of nest entrances were identical in the two treatments. This indicates that the number (and possibly the composition) of nests directly influence task allocation and foraging effort. Enhanced foraging via subtle effects on task allocation represents a new, previously undocumented benefit of polydomy.

The second foraging benefit evidenced in our study relates to the costs of searching for unknown food sources. We found that individual nests in polydomous colonies experience a significant reduction in search time (i) if they are close to a food source or (ii) if there is a sister nest *en route* to the food (experiment 2). In environments with scattered, unpredictable food sources, dispersed central-place foraging should therefore confer colonies with a dual benefit. First, spreading nests over a broader area increases the likelihood that at least one nest is located near a food source, which decreases search times for that nest (local benefit) [25,27,39]. Second, inter-nest communication allows farther-away nests to also benefit from discoveries by sister nests and experience lower search times (global benefit). Our results therefore indicate that polydomy can increase the foraging range not only of the colony as a whole, as discussed in previous studies [6,20,21,26,29,30,32,34,63], but also of individual nests, which gain easier access to far away resources via the presence of intermediary sister nests. This could be achieved either through information sharing (e.g. long-distance recruitment) or through food redistribution between nests. Both processes have been observed in polydomous ants (long-distance recruitment [23,35,38]; resource redistribution [23,24,36,38,40–44]) and may play a significant role in increasing foraging efficiency and homogenizing performance across nests [25,42].

In the first two experiments, we provided experimental support for foraging benefits associated with polydomy in food-deprived colonies. However, it is still unclear whether colonies become polydomous in response to heterogeneities in resource distribution, or whether enhanced foraging is only a positive side effect of polydomy. The experimental evidence available so far is inconsistent: some studies found that distant, stable food sources can trigger the foundation of new polydomous nests closer to these food sources [23,36], whereas other studies failed to reveal such an effect [33,64]. Additionally, these studies did not investigate the effect of the presence or absence of specific food types (e.g. proteins or carbohydrates) near the home nest on the likelihood of colonies to found new polydomous nests. Contrary to our predictions, we found that colonies which lacked a key dietary element near their home nest were not more likely to become polydomous than colonies that had a complete diet available near their home nest. Dietary requirements and spatial heterogeneity of resources therefore do not appear to trigger polydomy in *T. nylanderi*; in other words, foraging benefits may well be a positive consequence of polydomy without

being the reason for the foundation of new nests. Instead, polydomy may result from constraints on nest size: as *Temnothorax* species live in small natural cavities such as hollow acorns or rotten twigs, a single nest may be too small to accommodate growing sexual brood in spring and early summer [20,21,64–67]. Polydomy has also been suggested to act as a thermoregulatory mechanism [20,21,31,68,69], a bet-hedging strategy decreasing a colony's vulnerability to external risks [20,21,32,70], or a means for workers to escape queen control in intra-colonial reproductive conflicts [20,21,26,71–73]. All these factors combined may contribute to trigger the foundation of polydomous nests in spring in *Temnothorax* species.

Analysis of queen, brood and worker movement in experiment 3 however revealed that *T. nylanderi* colonies detect and adaptively respond to spatial heterogeneities in the distribution of different food types relative to available nest sites. Colonies that lacked a key dietary element near their home nest increased the relative occupancy of the outstation near the missing food type. This presumably increases their ability to defend and/or successfully retrieve the less-accessible resource [6,20,21,34,46]. In addition, colonies preferred to move brood and the queen towards the nest near the protein source irrespective of treatment. Previous studies on the dietary requirements of different castes in ant colonies revealed that the queen and larvae rely on protein-rich food for growth and egg production, whereas the workers' diet has a higher carbohydrate content [74,75]. In agreement with dispersed central-place foraging theory, moving brood and the queen towards a nest close to a stable protein source or to an area with high protein productivity should therefore be beneficial, because it decreases the costs of transporting protein-rich food towards its main consumers [22,23,36].

5. Conclusion

Overall, our study supports the long-standing claims that polydomy enhances foraging by stimulating foraging effort (experiment 1), decreasing food search times through a combined effect of increased effective foraging territory and inter-nest communication (experiment 2), and adjusting the location of colony members in heterogeneous environments according to their needs (experiment 3). Interestingly, social vertebrates that forage collectively appear to follow similar strategies as ants even though they usually have a less altruistic social system. Inter-individual voluntary communication about food location is predicted to be beneficial when resources are ephemeral, but locally abundant [76], and has been reported in multiple species of birds and mammals (reviewed in [77]). Similarly, fission–fusion dynamics allow social mammals to adjust group size and composition according to resource availability and individual needs [78]. For example, elephants, spider monkeys and chimpanzees form smaller social groups and increase the size of their territory when resources are limited [79,80]; ruminants tend to form sexually segregated groups because optimal time and resource allocation differ between sexes [81]. Polydomy and fission–fusion dynamics therefore appear to provide similar solutions for flexible resource exploitation in heterogeneous, variable environments.

Data accessibility. Data are available from the Dryad Digital Repository: (<http://dx.doi.org/10.5061/dryad.dj5d3>) [82].

Authors' contributions. N.S., P.J. and L.K. conceived the study and designed the experiments. N.S. and P.J. carried out the experiments. N.S.

analysed the data and wrote the manuscript. All authors commented on the manuscript and gave their final approval for publication.

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