A Recruit's Dilemma:

Collective Decision-Making and Information Content in the Ant *Temnothorax rugatulus*

by

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ABSTRACT

An insect society needs to share information about important resources in order to collectively exploit them. This task poses a dilemma if the colony must consider multiple resource types, such as food and nest sites. How does it allocate workers appropriately to each resource, and how does it adapt its recruitment communication to the specific needs of each resource type? In this dissertation, I investigate these questions in the ant *Temnothorax rugatulus*.

In Chapter 1, I summarize relevant past work on food and nest recruitment. Then I describe *T. rugatulus* and its recruitment behavior, tandem running, and I explain its suitability for these questions. In Chapter 2, I investigate whether food and nest recruiters behave differently. I report two novel behaviors used by recruiters during their interaction with nestmates. Food recruiters perform these behaviors more often than nest recruiters, suggesting that they convey information about target type. In Chapter 3, I investigate whether colonies respond to a tradeoff between foraging and emigration by allocating their workforce adaptively. I describe how colonies responded when I posed a tradeoff by manipulating colony need for food and shelter and presenting both resources simultaneously. Recruitment and visitation to each target partially matched the predictions of the tradeoff hypothesis. In Chapter 4, I address the tuned error hypothesis, which states that the error rate in recruitment is adaptively tuned to the patch area of the target. Food tandem leaders lost followers at a higher rate than nest tandem leaders. This supports the tuned error hypothesis, because food targets generally have larger patch areas than nest targets with small entrances.

This work shows that animal groups face tradeoffs as individual animals do. It also suggests that colonies spatially allocate their workforce according to resource type. Investigating recruitment for multiple resource types gives a better understanding of exploitation of each resource type, how colonies make collective decisions under conflicting goals, as well as how colonies manage the exploitation of multiple types of resources differently. This has implications for managing the health of economically important social insects such as honeybees or invasive fire ants.

DEDICATION

I dedicate this dissertation to my God, who is God from eternity to eternity, whose faithful love endures forever, and who keeps His Word.

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TABLE OF CONTENTS

Page

CHAPTER

Page

APPENDIX

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Social animals communicate with each other about the location of resources such as food and shelter. They may benefit from sharing other information about the target, such as type or quality of the resource. This could help manage the groups manage tradeoffs (Davies et al. 2012) between multiple resource types and optimize the spatial allocation of its workforce for each resource type. Here, I investigate these questions in a social insect colony. An insect society requires communication between its members to share information and function as a group (Seeley 1995; Hölldobler and Wilson 2008). Recruitment, a key type of communication, “brings nestmates to some point in space where work is required” (E. O. Wilson 1971). Social insects utilize recruitment to allocate foragers, or to emigrate, among other things (Hölldobler and Wilson 2008). For a colony to maintain its homeostasis for sustenance and reproduction, it must 1) allocate foragers to gain energy, and it also must 2) often emigrate to live in a suitable shelter, especially in social insects with fragile nests (Pratt 2010) and those that reproduce by colony fission (Seeley 2010). Information shared through recruitment is critical for a colony to effectively manage its workforce for such tasks. Thus, recruitment and resulting decision-making has been studied extensively in many species for foraging (Beckers et al. 1990; Seeley 1995; Beekman and Dussutour 2009) and for emigration (Beekman and Dussutour 2009; Pratt 2010; Seeley 2010; McGlynn 2012). But few studies have compared food recruitment and nest recruitment (Hölldobler 1971; Hölldobler, Möglich, and Maschwitz 1974; Hölldobler and Wilson 1978), and how the two recruitment systems are managed differently.

The system

Temnothorax rugatulus, which lives in fragile nests such as rock crevices, is an ideal choice of species for addressing this question for several reasons. First, *Temnothorax* is one of two model groups for house hunting, along with honeybees (Dornhaus et al. 2004; Beekman and Dussutour 2009; Pratt 2010; Seeley 2010). It has also been studied during foraging (Gottlieb et al. 2013; Shaffer, Sasaki, and Pratt 2013) and recruits readily in both situations. Second, it is better suited to address this question than the honeybees, because unlike bees which emigrate and forage in separate stages (Tanner and Visscher 2006; Seeley 2010), *Temnothorax* ants can emigrate from an intact nest (Dornhaus et al. 2004), and thus may need to simultaneously perform both activities. Third, *T. rugatulus* has advantages over other ants with bigger colonies (McGlynn 2012), because the whole emigration event can be studied in detail due to its small colony size (Möglich 1978), and nest site attributes can easily be manipulated (Pratt and Pierce 2001). It also uses tandem run recruitment (Möglich 1978), where the recruiter leads a single follower to the target, which allows each recruiter to be studied in detail, as well as its effect on recruited nestmates. Tandem running is used in several ant genera, across three subfamilies, to recruit to food, to nest or to an area to defend against an enemy (Hölldobler and Wilson 1990). Typically, a scout comes back to nest from a target and displays to nestmates (Traniello and Hölldobler 1984). Once a scout gets a follower, it leaves the nest toward the target. The scout, or the tandem leader, moves forward when the follower touches the hind part of the leader. If the follower loses contact with the leader, the leader stops and waits until the follower reaches and touches it again (Hölldobler and Wilson 2008).

Differences in behavior of food recruiters and nest recruiters

To understand how a colony uses recruitment to balance its workforce between foraging and emigration, I studied tandem running in *T. rugatulus* for both contexts. I hypothesize that tandem running is used to share important information that aids in colony management. Hence, I predict that there will be differences in food and nest recruiters that reflect the nature of the two tasks. In Chapter 2, I first investigated if there are differences in recruitment behavior between food and nest recruiters in *T. rugatulus*, which could be related to colony management. I discovered two new behaviors by these recruiters, and food recruiters performed these behaviors more often than nest recruiters. I did not, however, find an effect of these behaviors on their recipients, which leaves questions to address about these behaviors.

Food and nest recruiters could behave differently for several informational reasons: first, to be used by nestmates to distinguish and respond differentially to those contexts and second, navigational information to the target. I investigated these two possibilities to understand how the colony manages information transfer differently by context, which would reflect the balance between contexts.

Tradeoff between foraging and emigration

Whether and how the colony balances its workforce between foraging and emigration is important to study, because a colony must effectively use its workforce across many tasks, such as foraging, emigration, and defense, among other things. This is analogous to the foraging-predation risk trade-off (Sih 1980; Houston, McNamara, and Hutchinson 1993), where feeding animals balance weights on foraging effort and the predation risk that comes from foraging instead of staying in a safer area. In ants, this question is unknown but relevant: *Monomorium pharaonis* can use foraging recruitment trails for emigration (Evison, Fenwick, and Hughes 2012), while *Leptogenys distinguenda* discriminates foraging and emigrating trails (Witte and Maschwitz 2002). For a colony to balance foraging and emigration through recruitment, its workforce must be able to respond differently to the two contexts. I predict that 1) when nestmates are motivated to a certain context, they will follow more of recruiters to that context (Gottlieb et al. 2013; Shaffer, Sasaki, and Pratt 2013; Pratt and Sumpter 2006). I then predict that an increase in foraging effort will result in a decrease in emigration effort, and vice versa.

In Chapter 3, I presented *T. rugatulus* colonies both food and new nest targets, while manipulating colony motivation to each target to pose a tradeoff between the two targets for the colony. The colonies responded according to the predicted tradeoff through recruitment and visitation to each target, even though exploration level remained mostly constant through the experiment period. Studying recruitment in different contexts will bring new insight to decision-making, as there are differences in decision-making patterns between contexts in bees (Beekman and Dussutour 2009) and in *T. rugatulus* (Shaffer, Sasaki, and Pratt 2013).

How to bring a recruit to the target

When the recruiter shares information about the location of a target, there are two things to consider: first, how precisely should it lead the recruits to the location of the target? Second, once the recruits arrive at the target, how would they return to that target on their own? In Chapter 4, I investigated both of these questions in the ant *T. rugatulus*. The first question is relevant in social insects, because recruitment is often imprecise

(Deneubourg, Pasteels, and Verhaeghe 1983; Haldane and Spurway 1954; Towne and Gould 1988). This provides an opportunity to test the tuned error hypothesis, originally developed for honeybees (Weidenmüller and Seeley 1999), which suggests that directional error in recruitment is adaptively tuned. One prediction is that a target with a wider patch area will elicit greater directional error that would spread the arrival of recruits evenly; recruitment to a food patch will have greater directional error than recruitment to a nest site, a point source defined by a small entrance (Weidenmüller and Seeley 1999). This makes sense in a decision-making perspective as well, in relation to speed-cohesion trade-off (Sumpter and Pratt 2009); greater cohesion at one nest site will result from a more precise recruitment. However, this hypothesis has yet to receive empirical support (Preece and Beekman 2014). I investigated the paths of food tandem runs and nest tandem runs to test this hypothesis, and tested the prediction about directional error above. Indeed, food tandem runs were more likely to lose followers than nest tandem runs. Also, colonies with food targets started tandem runs earlier (controlling for time of target discovery) than those with nest targets, which could be because food tandem leaders do not invest as much time learning the route for to increase the success rate as nest tandem leaders do (Glaser and Grüter 2018).

The second question is, once the recruits arrive at the target, how would they return to that target on their own? When a tandem run ends, the follower needs to navigate subsequent routes alone (Pratt et al. 2002), so it is critical for the follower to learn visual or other navigational cues during the tandem run. Studies about learning such cues during recruitment, where followers need to navigate independently, are missing. Even in well-studied trail-laying ants, there are a relatively small number of studies indicating the effect of trails on visual learning (Hölldobler 1976; Klotz 1987; Harrison et al. 1989; Aron et al. 1993; Grüter, Czaczkes, and Ratnieks 2011; Czaczkes et al. 2011; 2013; Grüter et al. 2015). I tested the hypothesis that tandem followers learn the route during following by presenting previous tandem followers with either of two treatments on their subsequent solo trip: a block treatment in which I blocked the visual surroundings with a cardboard cylinder until they reached the target feeder, or a control treatment in which I briefly blocked the visual surroundings with the same cylinder but took it away soon after the ants began their lone trips. The ants with blocked surroundings during subsequent lone trips deviated from their tandem paths at a similar level as control ants, rejecting a role of visual learning during tandem runs. However, control ants were straighter in their lone trips than blocked ants, affirming the role of visual cues in navigation.

CHAPTER 2

INFORMATION SHARING IN TANDEM RUN RECRUITMENT

Abstract

Social animals often share information to distribute the workload of finding, exploiting, or defending a resource, or to otherwise enhance the benefits of group living. When looking for food or a new home, social insects use recruitment to enlist the help of nestmates by sharing the target's location. There is evidence that recruiters vary their recruitment behavior to indicate target quality, but it is unknown whether recruiters modulate a specific behavior to indicate target type. I hypothesized that the recruiters in the ant *Temnothorax rugatulus* share information about target type (food vs. nest) and target quality. I focused my investigation on the behavior of recruiters inside the original home nest (just before starting a tandem run recruitment), because this is when recruiters interact with the greatest number of ants. I discovered two new behaviors that the ants perform on nestmates: shaking display (moving the body in a fast and forceful burst in several directions) and vigorous antennation (rapid antennation in wide angles). Food recruiters perform a higher number of shaking displays and a higher number of vigorous antennations than nest recruiters, which suggests that the recruiters convey target type information to nestmates. When I observed the recipients of these behaviors and compared their response to that of the controls, though, the recipients did not show an increased response to foraging or other behaviors related to recruitment. When I investigate quality in two contexts, I used a common scale to compare food targets and nest targets: the probability that a target visitor recruits and report this probability for each target I used. I also found an interaction between context and target quality for

vigorous antennation: food recruiters did not vary the number of vigorous antennations with feeder quality, but nest recruiters did so with nest quality. This merits further study to find out whether and how the nestmate recipients use this available information, and how this affects colony decision-making when these various targets are presented simultaneously.

Introduction

Recruitment in social insects encompasses a range of methods by which an informed worker summons nestmates to help with tasks such as exploiting a food source, assessing a nest site, or fighting an enemy (E. O. Wilson 1971). Recruitment allows a rapid concentration of effort on a localized target, but it can convey more than just the place where work is required. Firstly, recruitment can communicate target quality. Recruiters may vary their behavior according to the profitability of the food source or the desirability of the nest site they have found (Hangartner 1969; Roces, Tautz, and Hölldobler 1993; Roces and Núñez 1993; Roces and Hölldobler 1996; Hölldobler 1999; Seeley, Mikheyev, and Pagano 2000; Seeley 2003; Cassill 2003; Richardson et al. 2007; Schmidt et al. 2008; Beekman and Dussutour 2009; Hrncir 2009). Recruits can respond to this variation in ways that help the colony reach consensus on the best of several options or allocate effort according to option quality (Szlep and Jacobi 1967; Verhaeghe 1982; Roces and Núñez 1993; Liefke, Hölldobler, and Maschwitz 2001; Cassill 2003).

Secondly, recruitment can convey the type of target. For example, some ants vary their recruitment method according to target type (Hölldobler 1971; Hölldobler 1980; Hölldobler 1984; 1999; Hölldobler, Möglich, and Maschwitz 1974; Hölldobler and Wilson 1978), such as laying pheromone trails to food sources but leading tandem runs to nest sites (Hölldobler 1980, 1984). This variation potentially allows the colony to optimize allocation of its workforce among competing priorities, including food collection, nest finding, or colony defense. This could be especially valuable when there is an asymmetry in need for different types of target. Competition among target types can happen when a colony is simultaneously foraging and scouting for new nest sites

(Beekman and Dussutour 2009; bees: Dyer 2002; Seeley 2010; in various ants: Longhurst and Howse 1979; Hölldobler 1999; Evison et al. 2012; Shaffer et al. 2013). In *Camponotus socius* and *C. sericeus*, recruitment to nests and to food activates different groups of ants (Hölldobler 1971; Hölldobler, Möglich, and Maschwitz 1974), suggesting that variation in recruitment behavior between contexts sends a message to potential recruits. Besides the two studies, few studies investigated whether any social insects modulate a specific recruitment behavior to indicate target type (Hölldobler and Wilson 1978).

Still less is known about how recruitment behavior changes when both target type and target quality vary. A colony's allocation of effort between distinct targets should depend not only on the target's type (say nest vs. food), but also their respective quality. This question has been little explored, but answers could give novel insight about the nature of foraging and emigration. In waggle dance recruitment by honeybees, food and nest recruiters use different rules when modulating the number of waggle runs (a proxy for quality; Seeley et al. 2000; Seeley 2003; Visscher 2007). This discovery was inferred to reflect the differing need for consensus in the two contexts: it is important for a house-hunting colony to move together to a single new nest, but the colony does better to allocate its foragers across multiple sources (Visscher 2007).

In this study, I ask how context and quality influence recruitment by the ant *Temnothorax rugatulus*. This species recruits via tandem runs, in which an informed ant leads a single nestmate to the target. They use tandem runs in colony emigrations, where the target is a potential new home, and also while foraging, where the target is a rich food source. In both contexts, ants are affected by target quality, showing a higher probability of initiating recruitment to better targets (Pratt 2010; Shaffer, Sasaki, and Pratt 2013), a sensitivity that helps the colony make adaptive collective decisions. Beyond this, there is no evidence to date that recruiters modulate their tandem runs according to either the type or quality of target, except that tandem runs to better nests are more persistent (Richardson et al. 2007). However, little work has been done on a likely venue for such modulation—the interactions between recruiters and potential recruits inside the home nest. In many ant species, when a recruiter returns to the nest from the target, she engages in various displays and interactions with nestmates (Hölldobler 1971; Hölldobler et al. 1974; Buschinger and Winter 1977; Stuart and Alloway 1983; Traniello and Hölldobler 1984; Maschwitz et al. 1986; Liefke et al. 2001), some of which are known to prime their response to recruitment (Szlep and Jacobi 1967; Hölldobler 1971; Hölldobler 1981; Möglich and Hölldobler 1975; Topoff and Mirenda 1978; Lenoir and Jaisson 1982; Hölldobler and Wilson 1990; Detrain and Pasteels 1991).

I hypothesize that recruiters convey information about target type and quality behaviorally, and that target type and quality interact to influence recruitment. To test these hypotheses, I presented *T. rugatulus* colonies with each of four different recruitment targets: poor food, good food, poor nest, and good nest. I compiled ethograms of the in-nest behavior of all recruiters to these targets, and I compared their behavior to detect target-dependent variation. I also looked at the behavior of ants that interacted with the recruiters, to test whether any recruiter actions toward these ants increased their participation in nest site exploration or foraging.

Methods

Subjects

I collected *T. rugatulus* colonies from the Pinal Mountains in Arizona (N 33° 19.00' W 110° 52.56'). Foraging experiments were carried out in October-November of 2015, using six colonies that had been collected between 2012 and 2014. Emigration experiments were done in March-May of 2016, using six colonies that had been collected in October 2015. Most colonies had one queen (a single colony had three queens); worker populations ranged between 75 and 250, and brood populations between 25 and 175. I used a different set of colonies to measure the recruitment probabilities associated with different quality food and nest targets (see below). For food targets, experiments were done in June-November of 2015, using six colonies collected in May 2014. For nest targets, experiments were done in March 2016, using 15 colonies (roughly half of which had multiple queens) collected between 2012 and 2015.

I maintained colonies as described in Sasaki et al. (2015), feeding them an agar-based diet (Bhatkar and Whitcomb 1970) and housing them in nests made of a balsa slat sandwiched between two microscope slides (50 X 75 mm). For most of the year, I housed colonies on laboratory benches or in an incubator with a 14:10 L:D light cycle, at approximately 22 °C and 15 °C (light and dark periods, respectively). I overwintered all colonies (except for colonies used to measure food recruitment probabilities) for several weeks in an incubator or refrigerator at 5 to 15 °C, to simulate winter conditions in the field. Colonies were returned to normal conditions at least one month before experiments.

Behavior of food recruiters

To study recruitment to food, I first motivated the ants by depriving them of food for 15-26 days (these ants are highly resistant to food deprivation (Rueppell and Kirkman 2005)). I then placed a hungry colony, in its nest, in a square 50 X 50 cm plastic arena and left it there for 2-24 hours to acclimate, explore the arena and to learn visual cues for navigation. I started the experimental trials between 12:00 pm and 6:00 pm by presenting the ants with 0.1 ml of sucrose solution in a glass depression slide about 30 cm away from the nest entrance. I placed either poor-quality food (0.1 M sucrose) or good-quality food (1.0 M sucrose) in the feeder. I recorded each trial with three video cameras: one gave a close view of the nest, another gave a close view of the feeder, and the third gave a view of the whole arena. I recorded until I observed at least two tandem runs, up to a maximum of 3 hours after the feeder had been presented. I observed each of six colonies twice, once with poor food and once with good food. To account for any order effects, I gave three colonies the good treatment first, and I gave the other three the poor treatment first.

Using the video recordings, I made detailed descriptions of the behavior of each tandem recruiter from the time that she entered the nest after returning from the feeder, until she left the nest to lead a tandem run. I observed a total of 10 recruiters to 0.1 M sucrose and nine recruiters to 1.0 M sucrose. I observed only one nest visit per recruiter to avoid pseudo-replication. Foragers were easy to spot because their gasters were distended with sucrose solution, and every recruiter I observed performed trophallaxis (food sharing with nestmates) before leading a tandem run. I omitted some recruiters who led tandem runs before I presented the feeder, because they must have been heading toward an unknown target.

Behavior of nest recruiters

To study nest recruitment, I first gave ants the opportunity to acclimate and to learn visual cues for navigation by placing a colony, in its home nest box, on the bench location where experimental trials were carried out. After 0 to 100 min, I then transferred the colony, in its nest, to the same 50 X 50 cm arena used for the foraging experiment. I started the trial between 10:30 am and 4:30 pm by removing the roof of the ants' home nest to motivate emigration. About 10 min later I placed a single new nest, of either poor or good quality (see details below), about 30 cm from the home nest entrance. I recorded each trial with three video cameras: one gave a close view of the home nest, another gave a close view of the new nest, and the third gave a view of the whole arena. As in foraging experiments, I recorded until I observed at least two tandem runs. For those colonies that yielded data, this took up to 2 hours 15 min after presentation of the new nest. In two trials, colonies did not start emigrating to the new nest for more than five hours, so I waited up to 20 hours until they emigrated, but I did not record any tandem runs from these trials. One colony emigrated within two hours in both of its trials, but did not yield any recruiters that I could analyze, so I took this colony out from analysis. After each trial, I induced colonies to move back into their original nest by restoring its roof and removing the roof of the newly occupied nest. This ensured that all colonies began each trial in the same type of nest, regardless of their choice in a previous trial.

As in foraging experiments, I used each of six colonies at least twice, once with a poor nest and once with a good nest. To account for order effects, I gave two colonies the good treatment first, and I gave another two the poor treatment first. Two trials with poor treatment did not yield any recruiters that I could analyze, so I used two other colonies: I gave each of these colonies alternating treatments starting with the poor treatment, until they yielded recruiters from poor treatments on their third trial. I rested colonies for 14-29 days before each of their trials. Thus, of the six colonies, two yielded data for both nest types and the other four for only one type each (see Appendix A: Table S1 for details).

As in the foraging experiment, I used the video recordings to compile a detailed behavioral record of each recruiter's visit to the home nest preceding her tandem run. I observed two ants from each trial, for a total of eight recruiters to the good nest and eight recruiters to the poor nest. To avoid pseudo-replication, I observed only one nest visit per recruiter. I reviewed video recordings to ensure that all 16 tandem runs were indeed directed to the new nest, rather than some other target. Some tandem runs broke up before reaching the new nest, but I nonetheless counted them as heading there if the leader had visited the new nest just before starting the tandem run. Tandem leaders were excluded from analysis if I saw them carrying a nestmate during the tandem run or if they led a reverse tandem run (i.e., one from the new nest to the home nest) before entering the home nest to find a follower. I did not use blinded methods for observing these recruiters, because I were looking for new behaviors, which made standardizing these behaviors across observers difficult.

Nest designs

I designed good and poor nests to differ strongly in three attributes known to affect emigration decisions in *Temnothorax*: entrance size (smaller is preferred), nest cavity size (larger is preferred), and interior light level (dimmer is preferred; Pratt and Pierce 2001; Franks et al. 2003). For each nest, I placed a 2.4 mm-thick balsa wood slat between two glass microscope slides (50 X 75 mm). I cut a rectangular cavity into the slat, accessible to the ants by an entrance tunnel through one side. The poor nest had a circular cavity at 40 mm in diameter and a 4 mm wide entrance tunnel, while the good nest had a rectangular 40 X 65 mm cavity and a 1 mm wide entrance tunnel (Fig. 2.1; drawn in Inkscape (Inkscape Project 2017)). To dim the cavity interior of the good nest, I placed three 3-stop neutral density filters (Rosco Cinegel) between two microscope slides and placed these slides on top of the nest. I expected this to dim the nest interior by as much as a factor of 512 relative to the poor nest, which had no filters on its roof. However, the actual reduction was less than this maximum, because some light also enters the nest via the floor and entrance. To obtain a direct measure of interior light level I used an illuminance meter equipped with a small probe (Minolta T-10). For each nest type, I assembled a nest as normal but replaced the floor with an opaque cardboard slat in which the illuminance meter's probe was embedded. I then placed this nest in the experimental arena under the conditions used during the experiment (fluorescent overhead lighting), and noted the illuminance detected by the probe. These measurements captured light entering through the nest's glass roof. To quantify light penetration through the glass floor, I repeated this measurement, except that I replaced the roof (rather than the floor) with the cardboard slat with embedded probe. I summed the two measurements to estimate total illumination of the good nest cavity as 5 lux and the poor nest cavity as 463 lux. Previous experiments indicate that colonies of *T. rugatulus* reliably discriminate this difference when choosing between nests (Sasaki et al. 2013).

Recipient behavior and controls

I discovered that recruiters performed two new behaviors toward other ants in the nest: shaking displays and vigorous antennations (details in results). I hypothesized that these behaviors may serve to stimulate search or induce tandem following by their recipients. To test this, I observed recipients for 5 min following their interaction with the recruiter and recorded whether they engaged in trophallaxis, moved to the nest entrance, exited the nest, or followed a tandem run. For vigorous antennation, I got at least one recipient of vigorous antennation from each recruiter; I did not count recipients of vigorous antennation that later received shaking within 5 min.

I compared these data with similar observations of control ants followed for the same length of time. For controls I selected ants that the recruiter interacted with shortly before or after her shaking display or vigorous antennation. I scanned either forward or backward from the event in pseudorandom order, selecting the first ant that had not received either type of behavior, but which the recruiter otherwise contacted with its head or antennae. For shaking displays I selected one control ant for each recipient ant. I did the same for vigorous antennations by nest recruiters, but I observed controls for only a subset of vigorous antennations by food recruiters (six from poor food trials and eleven from good food trials, to match the numbers for poor and good nest recruiters, respectively). I did not select ants as controls if they performed trophallaxis with the recruiter.

To shed further light on the relation between in-nest experience and tandem following, I observed the behavior of each tandem follower to food during the five minutes immediately preceding the start of the tandem run. I picked food recruiters over nest recruiters, because I saw both shaking and vigorous antennation in food experiments, and therefore assumed that any behavior related to tandem following would be more pronounced in food experiments.

Quantification of target quality

In order to investigate the effect of target quality across contexts, I needed a common metric of quality applicable to both nests and food. Many factors influence an ant's assessment of quality, and these factors are different for nest sites (e.g., cavity volume) and food sources (e.g., sucrose concentration). However, prior studies on both kinds of recruitment have shown that visitors integrate multiple features of a target into a single, measurable behavioral response: the probability that a visitor to the target subsequently initiates recruitment (Pratt et al. 2005; Shaffer, Sasaki, and Pratt 2013). I estimated this probability for each of the four targets used in my experiments.

To measure recruitment probabilities to food, my method was as follows. I placed a nest containing a colony in a 22 X 22 cm arena and left it there overnight to acclimate. I then placed a glass depression slide 10 cm from the entrance of the nest and supplied it with a drop of sucrose solution. I observed the colony until exactly 20 visits had been made to this feeder. During this period, I also counted all tandem runs toward the feeder. After the 20th visitor returned to the nest, the feeder was removed to prevent further visits. I continued to observe the ants for approximately 10 minutes to catch any further tandem runs. I used six colonies total across the two sucrose strengths; for each sucrose strength, I conducted seven trials (some colonies were tested twice at a given strength). I then estimated recruitment probability by dividing the number of tandem runs observed across all seven trials by the total number of visits across all seven trials. This estimate assumes that each visit is followed by an independent decision to lead a tandem run or not. In fact, the decisions within a given trial are unlikely to be fully independent, because some visits were probably return trips by ants that had already fed. However, this issue affected all the sucrose strengths I measured, hence I do not expect it to introduce a bias. To ensure high and roughly equal motivation to feed, colonies were starved for 14-20 days before testing.

For recruitment probabilities to nests, I modified the above procedure as follows. I introduced a colony to a 50 X 50 cm arena, along with an unoccupied new nest approximately 10 cm from the home nest entrance. I then removed the roof of the home nest and recorded the subsequent emigration with a video camera mounted above the arena. I reviewed the video from the start of the emigration until 5 minutes after the 10th visit to the new nest. I counted all tandem runs that resulted from one of these first 10 visits. I used only 10 visits, because I wanted to confine my observations to the early part of emigration, before the colony reaches a quorum and switches from tandem recruitment to transport. Because the new nest remained in the arena after the 10th visit, I needed to ensure that I did not count any tandem runs that originated from later visits. I accomplished this by reviewing the video recording of every tandem run to determine whether its leader had left the new nest before or after the 10th visit; the latter tandem runs were not counted. I conducted seven trials for good nests and eight for poor nests, using a different colony for each trial. For each nest quality, I estimated recruitment probability by dividing the number of tandem runs observed across all trials by the total number of visits across all trials.

Statistical analysis

To test for effects of target type and quality on recruiter behavior in the nest, I fit generalized linear models. The response variable in each model was the count of shaking displays or vigorous antennations by each recruiter, and the predictor variables were the recruitment target type (nest or food) and quality (scored as recruitment probability). The two recruiter behaviors were modeled separately, but shaking displays were often accompanied by vigorous antennations. I analyzed these cases as shaking displays only, because body movement seemed dominant over antennal movement. Because the response variables were counts with a strong right skew, I used Poisson regression, after first testing the assumption that the mean and variance of the counts were similar (i.e., the data were not overdispersed). I fit full models that included type, quality, and their interaction, as well as simpler nested models. I then used analysis of deviance to select the most parsimonious models accounting for variance in each behavior. I also used Poisson regression to separately analyze food and nest contexts for an effect of target quality.

I tested for effects of shaking displays and vigorous antennations on the behavior of recipients. For behavior recorded as counts, I used Fisher's Exact test or the Cochran-Mantel-Haenszel test (CMH; Agresti 2012). The CMH test allowed us to compare the behavior of two groups (e.g., recipients and controls) while controlling for other factors (e.g., target quality or type). I also used the CMH test to compare recipient behavior in the foraging and colony emigration contexts, while controlling for recipient vs. control. For behavior recorded as durations, I used quasi-Poisson regression instead of poisson regression, as the data were overdispersed (Kleiber and Zeileis 2008). I otherwise repeated the same process described above for Poisson regression. I used R version 3.3.1 for all statistical analyses (R Core Team 2016).

Results

Quantification of target quality

The results indicate low recruitment probability values for the poor feeders and nest sites, and high values for the good feeders and nest sites, as expected, but feeders also had higher mean values than the corresponding nest sites (Fig. 2.2).

Recruiter interactions with nestmates

Upon returning from a feeder or nest site, a recruiter typically entered the home nest and interacted with nestmates before eventually leaving with a tandem follower (Fig. 2.3; see Appendix A: Online Resource 1-2 and Appendix A: Table S2 for comparison of visit duration; Dunn 1961, 1964; Holm 1979; Fox and Weisberg 2011; Signorell et mult. al. 2017). Interactions in the nest included trophallaxis (for food recruiters; see Appendix A: Online Resource 3 and Appendix A: Table S2 for comparison of trophallaxis duration) as well as two distinctive behaviors that have not previously been described in these ants. In *shaking displays*, the recruiter faced a nestmate and shook its body in a fast and forceful burst in at least 3 out of 4 directions: 1. left, 2. right, 3. forward and 4. backward movement. In *vigorous antennations*, the recruiter faced a nestmate and antennated her rapidly, with antennae moving in wider angles (several directions) than usual antennations. Some of these involved only 1 antenna.

Also, sometimes food recruiters appeared to stridulate, moving their gasters up and down at a regular rate, especially when doing trophallaxis as donors. It seemed that many recipients of trophallaxis were engaged in this as well, so this does not seem to serve an important role in recruitment, unlike stridulations in other ants (Markl and Hölldobler 1978; Baroni-Urbani, Buser, and Schilliger 1988; Roces, Tautz, and Hölldobler 1993; Roces and Hölldobler 1996).

Shaking displays

Food recruiters performed more shaking displays than nest recruiters (Fig. 2.4), which is supported by the Poisson regression model: the simplest and best-supported Poisson regression model included only a main effect of target type ($p = 0.0027$), with no main effect of quality and no interaction between target type and quality (Fig. 2.4, Appendix A: Online Resource 6). Finally, when I separately tested the two target types, I found no effect of quality on the incidence of shaking for either food recruiters ($p = 0.34$) or nest recruiters ($p = 0.34$).

Vigorous antennations

Vigorous antennations were also more common for food recruiters than nest recruiters, but the effect of quality was more complex (Fig. 2.5). The best-supported Poisson regression model was the full model including target type ($p = 0.00019$), food quality ($p = 0.63$), and their interaction ($p = 0.019$; Fig. 2.5, Appendix A: Online Resource 7). The significant interaction effect means that there was a significant effect of quality for nest, but not for food. In addition, when I separately tested the two target types, I found a significant effect of quality on the incidence of vigorous antennation for nest recruiters ($p = 0.0062$) but not for food recruiters ($p = 0.63$). Thus, I conclude that food recruiters are significantly more likely to do vigorous antennation than are nest recruiters, and that target quality also has a positive influence on the frequency of vigorous antennation, but only for nest recruiters.

Behavior of recipients vs. controls

I found no evidence for differences from controls in the behavior of recipients of either shaking displays or vigorous antennation. For shaking, I analyzed only food recruitment, because of the small number of shaking displays by nest recruiters. There were no significant differences between recipients and controls for any of the four behaviors examined, controlling for target quality (Table 2.1). There were also no significant differences between recipients and controls in the time spent doing trophallaxis (Quasi-poisson regression, $p = 0.79$; Appendix A: Online Resource 8) or standing in the entrance tunnel (Quasi-poisson regression, $p = 0.15$; Fig. 2.6, Appendix A: Online Resource 8). For vigorous antennations, there were also no differences between recipients and controls for any of the four behaviors, controlling for target type (Table 2.2).

Behavior of recipients in food vs. emigration contexts

I found some differences in the behavior of recipients of vigorous antennation between the food and emigration contexts (controlling for recipient vs. control). I saw significantly more trophallaxis in the food context, and significantly more movement to the nest entrance and exiting the nest for the emigration context. There were no significant differences for following tandem runs (Table 2.3). I did not examine shaking displays for this analysis, since there were so few for the emigration context. The above analyses tested for differences while controlling for the type of ant (recipient vs. control).

When I analyzed ant types separately, I found similar results for recipients, but controls showed a significant difference only for trophallaxis (see Appendix A: Table S3a and S3b). This suggests that vigorous antennation might contribute to the difference in moving to the entrance and exiting the nest seen in Table 2.3.

Behavior of recipients in emigrations to poor vs. good nests

The above analysis on recruiter behavior showed an effect of nest quality on the incidence of vigorous antennation. I tested whether this was accompanied by quality-dependent differences in the behavior of recipients, but found no significant differences for any of the four behaviors (Table 2.4).

Pre-tandem follower behavior

I tracked the ants that became tandem followers and counted the number of vigorous antennations and shaking displays that they received. The number was not very different between good food and poor food (Table 2.5), nor was the number of ants that received shaking displays or antennations (Table 2.6). I also recorded the behaviors of these pre-tandem followers (Table 2.7). Interestingly, 7 of 10 good food followers and 8 of 9 poor food followers were at the entrance tunnel even before interacting with the recruiter, indicating that the followers were somehow primed to exit the nest before any interaction with the recruiter. This is further supported by the observation that 3 of 10 good food followers and 4 of 9 poor food followers had exited the nest before following the recruiter. These pre-tandem followers were significantly more likely to move to the entrance and to exit the nest than recipients of shaking (none of which became tandem followers). As for trophallaxis, it was observed in 1 of 10 good food followers and 4 of 9 poor food followers.

Discussion

Recruiter behaviors: context

Our main finding is that context affects the behavior of recruiters in *T. rugatulus* ants: recruiters for food do more shaking displays to nestmates compared to recruiters for nest (Fig. 2.4). I also found that these food recruiters perform more vigorous antennations than nest recruiters (Fig. 2.5). The fact that food recruiters perform both behaviors more often suggests that the colony could get information about the type of target by detecting the difference in the frequency of the behaviors.

For shaking displays, I observed a total of 24 instances in food recruiters, while I observed a total of 4 instances (close to 0) in nest recruiters. Shaking instances that are mostly limited to foraging may serve a specific purpose, signaling to the recruitee that the recruiter is headed to food (such as in *Leptogenys distinguenda*, where the poison gland is added for foraging, while a group of workers bumped against nestmates for emigration; Witte and Maschwitz 2002). Note that there is an element of subjectivity in the criteria used to score a shaking display: because it includes several forceful bursts, and I did not use an accelerometer or a high-speed camera; I relied on the observer’s (JYC) scoring. But, the shaking displays I observed could be the same behaviors that other authors noted: the motor displays mentioned in Shaffer (2014), and could also be similar to “vibrating movements,” though these happened rarely, in Pohl and Foitzik (2013).

On the other hand, for vigorous antennations, I observed a total of 113 instances in food recruiters, while I observed a total of 45 instances in nest recruiters. The fact that both target types have sizeable numbers of vigorous antennations suggests that vigorous antennation may serve as a general invitation, regardless of target type, for nestmates to share the work with recruiters or to follow the recruiter on a tandem run: an additional attractant for potential followers, along with the pheromone from the poison gland (Möglich, Maschwitz, and Hölldobler 1974; Möglich 1979). Möglich (1978) does mention that recruiters rapidly antennate nestmates.

Information sharing about target type is relevant for collective decision-making, especially when colonies have to find food and nest simultaneously. This situation happens in *T. rugatulus* (personal observations), in army ants (Witte and Maschwitz 2002) and possibly in swarming bees, if the food-replete bees start to get depleted and require foraging, before they decide on a new nest (Tanner and Visscher 2006). Other ants that emigrate from intact home nests (McGlynn 2012) likely maintain foraging activities while emigrating, which can last several days or weeks (Rockwood 1973; Smallwood 1982; Tsuji 1988; Anderson and Mull 1992; Tschinkel 2014). In these situations, how does information sharing about the type of target affect colony recruitment and allocation to each target? According to Blüthgen and Feldhaar (2009), "food and nesting space are the most important resources in ant ecology," so it would be worth investigating how colonies respond to the need for both.

Recruiter behaviors: interaction between context and quality

For vigorous antennations, the effect of the interaction between context and quality was also significant, even though quality itself was not significant: recruiters for good food targets perform vigorous antennations at an equal level as those in poor food targets, but nest recruiters perform more vigorous antennations when recruiting to better nest targets. This suggests that nest recruiters share information about the quality of nest targets to nestmates. This follows examples of social insects that vary their recruitment behavior according to nest quality (Seeley 2003; Richardson et al. 2007), and vigorous antennations could be the mechanism by which better nests incur higher recruitment probability in *Temnothorax* (Pratt 2010). This could be similar to Liefke et al. (2001), where a more complex set of invitation behavior resulted in more followers.

This interaction effect would not have been found if I did not consider both context and quality. In fact, to my knowledge, this is the first experiment focusing on the influence of both context and quality on recruitment. More studies like this considering both in other systems are needed to learn more about how different systems respond. In fact, in honey bees, dancers for a food source and dancers for a new nest site both indicate quality of their respective targets, but in different ways: food dancers dance longer and livelier for a higher quality food source (Seeley, Mikheyev, and Pagano 2000), whereas nest dancers do more waggle phases for better nests (Seeley and Buhrman 2001; Seeley 2003). If the two types of dances, each type with quality variation, are investigated simultaneously, it is possible that I could observe an intriguing interaction between context and quality in these dances.

Recruitment probability as a common metric between foraging and emigration.

When I use recruitment probability as a common metric between the two contexts, I are assuming that a scale used in foraging is transferrable to emigration, and vice versa, i.e., a probability of 0.3 in food is comparable to a probability of 0.3 in nest.

One difference between foraging and emigration that influences the rate of recruitment is that in emigration, tandem recruitment switches to transport when a colony decides to move into a new nest, accelerating the speed of arrival to the new nest, whereas there are only tandem recruitments in foraging. This is not an issue for the recruitment probability I measured in this study, because for emigration, I restricted my measurement to the pre-transport phase (except for once in good nest treatment, which had a reverse tandem run ; this indicates that transport to the new nest has begun). Each tandem run in emigration is expected to increase arrivals of visitors to their respective target by the same amount, as is each tandem run in foraging (Pratt et al. 2002; Shaffer, Sasaki, and Pratt 2013).

Colony satiation during foraging reduces the probability of recruitment (Shaffer 2014), but this is not an issue for the recruitment probability I measured in this study, because I removed the feeder after the 20th visitor returned to the nest for each trial. In foraging, a colony could exploit multiple targets at the same time whereas in emigration a colony usually ends up moving into a single new nest. But this is not an issue here, because in my measurement, I only had one target in each trial. Colony hunger state and nest condition could affect the probability of recruitment to respective targets (Seeley 1995; Pratt and Sumpter 2006; Shaffer 2014), but in this study, in both foraging and emigration experiments, colonies were highly motivated for respective targets. Another potential criticism of using recruitment probability between foraging and emigration is that the scale in the two contexts are different; a probability of 0.3 for foraging might not mean the same as a probability of 0.3 for emigration, which could be the case.

For readers who have reservations about this assumption, I included an analysis on shaking that tests the context effects and quality effects separately, and the same type of analysis on vigorous antennations (Appendix A: Online Resource 9 and 10). I used binary values (poor vs. good) for quality in these analyses, instead of mean recruitment probabilities. Here, food recruiters did significantly more shaking displays than nest recruiters, while the effect of quality was not significant, as shown in the analysis using recruitment probabilities. Food recruiters also did significantly more vigorous antennations than nest recruiters. The effect of quality was significant for nest recruiters, but not for food recruiters, as shown for recruitment probabilities analysis. The overall effect of quality was significant in here, unlike the recruitment probabilities analysis.

Recipient behaviors

Recipients of shaking were equally likely as controls of shaking to engage in trophallaxis, to move to the entrance, exit nest, and follow a tandem run. If shaking signals that the recruiter is headed to food, then I predict that the recipients of shaking will engage in more foraging-related activity, such as trophallaxis (as tremble dance does in bees; Seeley et al. 1996), than controls of shaking. Since there are no differences, this could be because shaking is a modulatory signal: a signal that produces a small response by itself but makes the recipient more likely to do a certain behavior, in combination with the main signal (Markl and Hölldobler 1978; Nieh 1998; Hölldobler 1999). I did not test this prediction, because I recorded only 4 recipients who received both shaking and vigorous antennations.

Recipients of vigorous antennation were equally likely as controls to engage in trophallaxis, to move to the entrance, exit nest, and follow a tandem run. If vigorous antennation serves as a general invitation signal for its recipients, then I predict that its recipients will be more likely to follow a tandem run, or engage in similar behaviors, such as move to the entrance or exit nest. On the other hand, I did observe differences among ants in: trophallaxis (higher for recipients in food than those in nest), move to the entrance (higher for nest recipients), and exit nest (higher for nest recipients; Table 2.3). This suggests that context itself could make recipients in food and nest respond differently from each other: in food experiments, all of the recruiters did trophallaxis, the home nest was intact and had few, if any, ant transports; in nest experiments, few ants did trophallaxis, the home nest had its roof removed, and many ants did transports. Perhaps colony hunger motivates the ants to do trophallaxis, look for food or a food recruiter, whereas the degree of nest destruction informs the ants inside to head to the entrance and exit nest to look for a new nest or a nest recruiter. Differences in condition due to context can arise through other means such as spatial position (Topoff and Mirenda 1978) or odor of recruiters (Dornhaus and Chittka 1999; Thom et al. 2007).

I offer some general explanations on why I did not detect any predicted differences between recipients and controls or between good nest and poor nest recruiters:

1. *The probability of recipient response depends on the number of shaking or the number of vigorous antennations that the recipients received*, in a manner similar to *Pogonomyrmex barbatus* harvester ants that can respond to rates of encounter with other workers (Gordon and Mehdiabadi 1999). I could not test this idea, because the number of vigorous antennations/shaking each recipient received was mostly one (Appendix A: Online Resource 11).

2. *The recipients respond in a more subtle way, such as moving faster or moving more within the nest.*

3. *5-min observations on the recipients were too short*, and it takes longer for recipients to show observable response.

4. *Vigorous antennation or shaking display could serve a purpose other than what I tested for*, such as to increase the activity of ants that started trophallaxis, so that they continue sharing food for a longer time. This would explain the higher number of vigorous antennations in food recruiters compared to nest recruiters.

On the other hand, invitation behaviors may be more functional for group-recruiting ants that lead multiple nestmates to the target (*Leptothorax duloticus*, Wesson 1940; E. O. Wilson 1975): In *T. americanus*, which leads group recruitment, recruitment happened more often when scouts antennated nestmates (Pohl and Foitzik 2013).

What induces ants to follow tandem runs?

When I observed pre-tandem followers, a majority of them (15/19 food followers) were at the entrance tunnel even before interacting with the food recruiter. This suggests that some ants stand by the entrance and wait, whether for tandem leaders, returning foragers or are guarding the entrance. These waiting ants might represent a task group that consistently get involved in following tandem runs, as the group of ants in Pinter-Wollman et al. (2012) that get involved in emigration but not in other tasks. But, the pre-tandem followers I observed could be a relatively small subset of potential followers, because tandem leaders often attract and lead several ants before leaving the nest, usually with only one ant.

For tandem runs, it is possible that the pheromone from the poison gland (Möglich 1979) is all that is needed to get followers, because the pool of available tandem followers is much larger than the pool of available tandem leaders. The tandem leader usually recruits only one ant out of more than 100 ants in the nest, and tandem runs do not happen very often (about 1 tandem run per 3 min for foraging from Fig. 2.5 in Shaffer et al. (2013); about 1 tandem run per 8 min for emigration from Table 2 in Möglich (1978)).

In honey bee recruitment, dances for better feeders are longer and livelier (Seeley, Mikheyev, and Pagano 2000), but according to Seeley (1995), waggle runs for the better feeder and the poorer feeder are "equally attractive to dance-following bees." Seeley (1995) suggests that this way, dance followers respond to all dances (each of which is high-enough quality to elicit dancing) and are dispatched to a variety of food resources. This would be a better allocation than disproportionately allocating to the one best food resource, which could change at any time (Seeley 1995). Likewise, *T. rugatulus* recruiters show behavioral variation according to context and nest quality, but these behaviors do not make their recipients more likely to follow the recruiters. Instead, it may be that the observed variation in recruitment probability (this chatper; Pratt 2010; Shaffer et al. 2013) arises through the recruiters for more desirable targets showing greater persistence in successive recruitments (Visscher 2007), or spending longer time waiting for followers in the nest (But recruiters in good nest did not have longer visits than those in poor nest; Appendix A: Table S2).

Conclusion

I found two new behaviors performed by recruiters in the home nest before recruitment: shaking displays and vigorous antennation. These recruiter behaviors vary by context as I expected, as well as by the interaction between context and quality.

However, it is not yet clear what the impact of these behaviors is on the recipients or the colony.

Fig. 2.1. 3D representation of nest designs used in colony emigration experiments. Good nest (top): entrance area = ~ 1.5 mm^2, cavity volume* = ~ 5.2 ml, light level in the nest = 4.99 lux. Poor nest (bottom): entrance area = ~ 8 mm^2, cavity volume* = ~ 2.5 ml, light level in the nest = 463.3 lux (* Both estimating the height is ~ 2 mm).

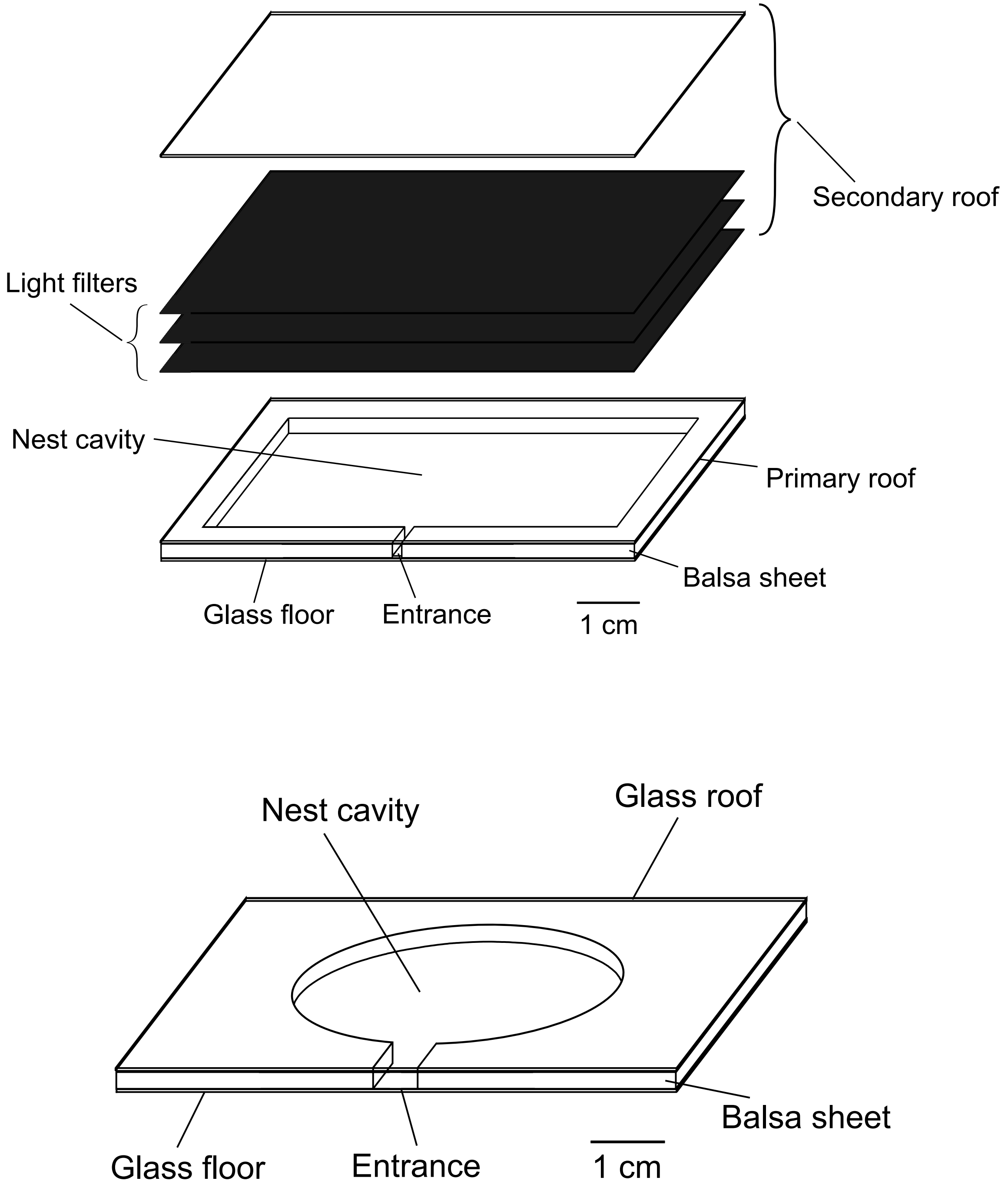


Fig. 2.2. Estimated recruitment probability by target type and quality. Blue squares indicate food targets, and red squares indicate nest targets. Brackets show 95% confidence intervals calculated by the Wilson interval method (E. B. Wilson 1927; Agresti and Coull 1998; Signorell et mult. al. 2017).

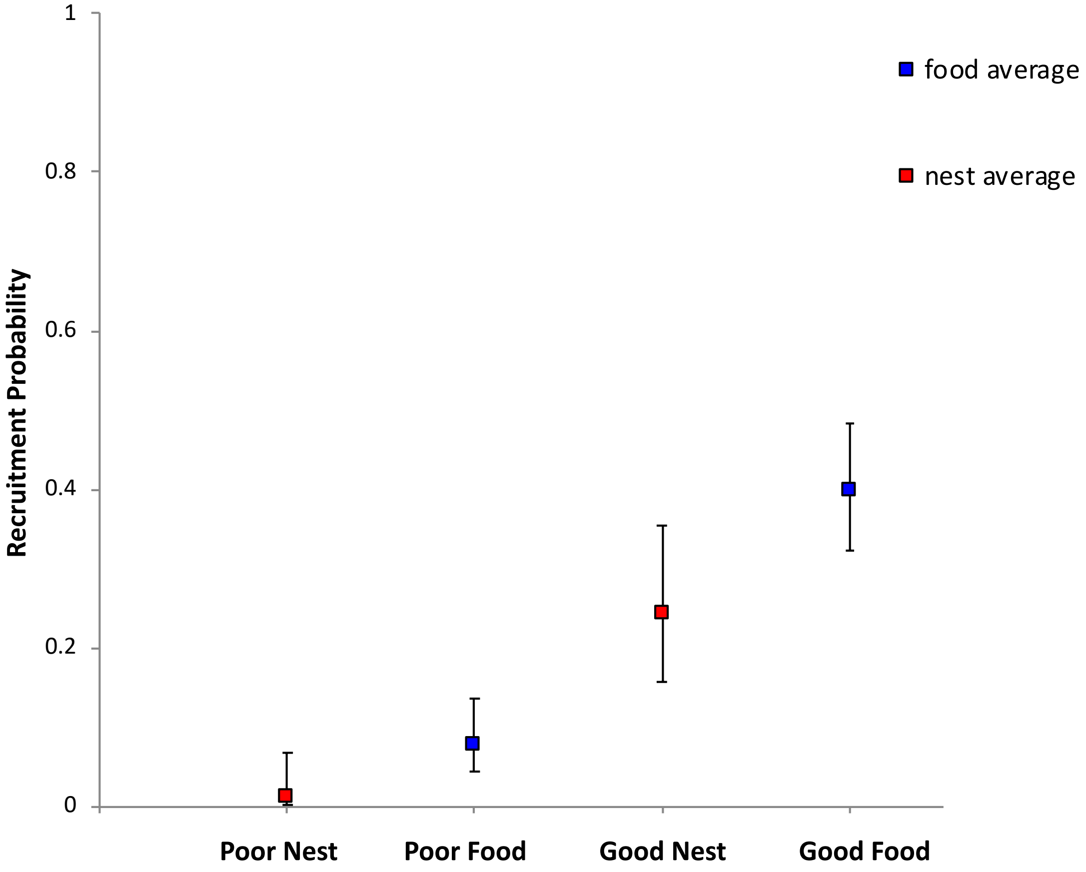


Fig. 2.3. Timeline of the behavior of 4 recruiters in each target: a. Poor food, b. Good food, c. Poor nest, and d. Good nest. Time is 0 when the recruiter is entering the home nest.

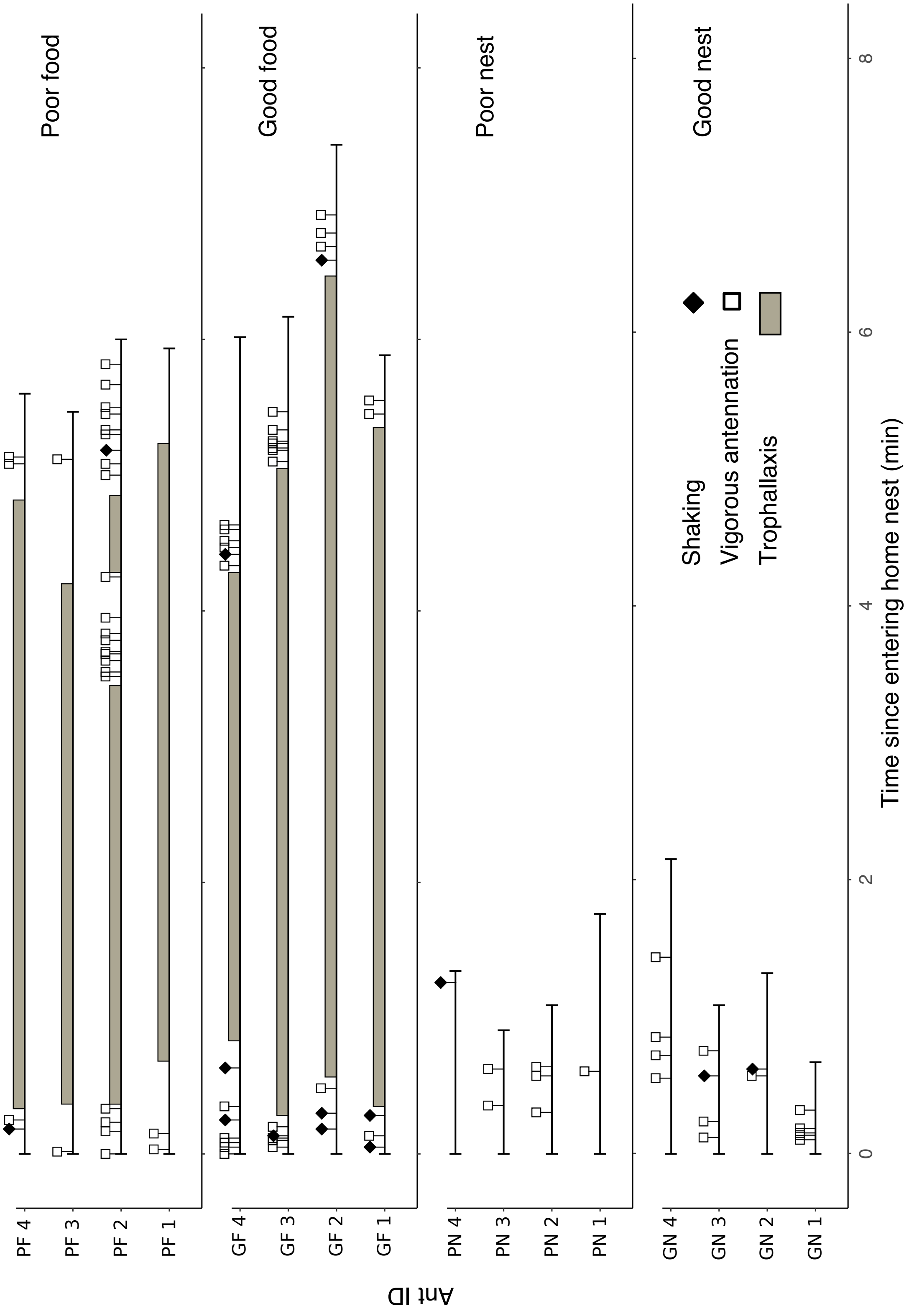


Fig. 2.4. The number of shaking displays by target type and quality (quantified by mean recruitment probability). Data for food recruiters and nest recruiters are shown in red and blue squares, respectively. Small symbols show counts for individual recruiters and large squares show averages. For each of the four targets, random vertical jitter is added to better show the data (total N = 35). The best-supported Poisson regression includes only a main effect of target type (*p* = 0.0027), and quality and the interaction between target type and quality are not important for the data.

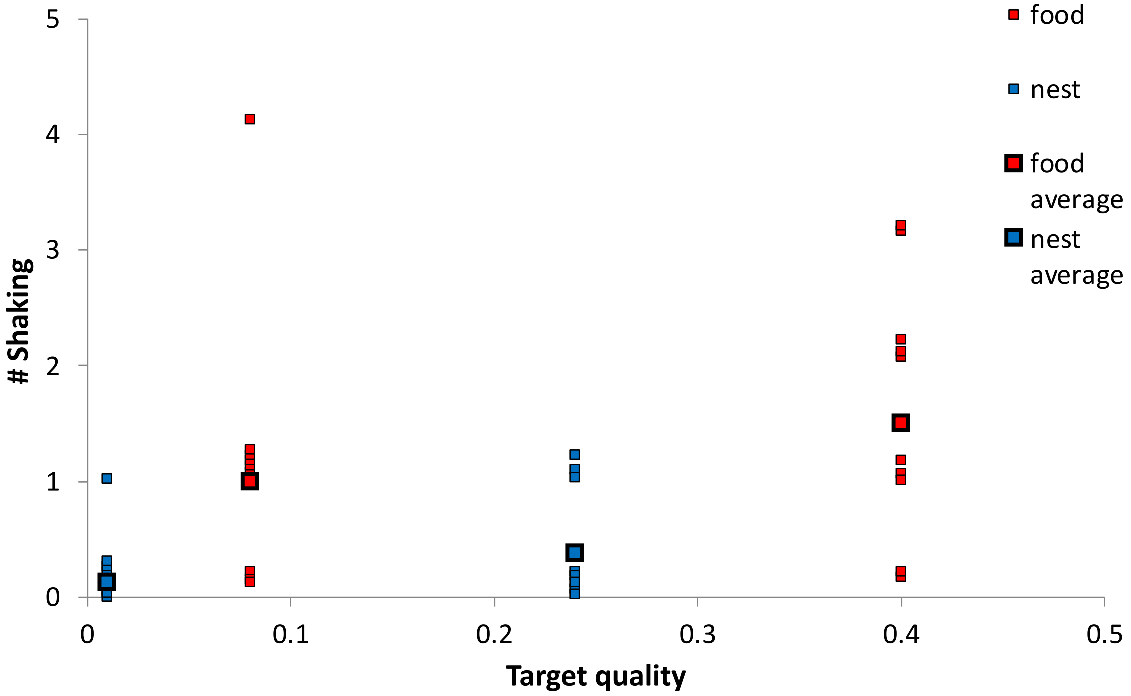


Fig. 2.5. The number of vigorous antennations by target type and quality (quantified by mean recruitment probability). Data for food recruiters and nest recruiters are shown in red and blue squares, respectively. Small symbols show counts for individual recruiters and large squares show averages. For each of the four targets, random vertical jitter is added to better show the data (total $N = 35$). The best-supported Poisson regression includes: target type ($p = 0.00019$), food quality ($p = 0.63$; the regression includes food quality instead of quality because of the added interaction between target type and quality), and the interaction between target type and quality ($p = 0.019$).

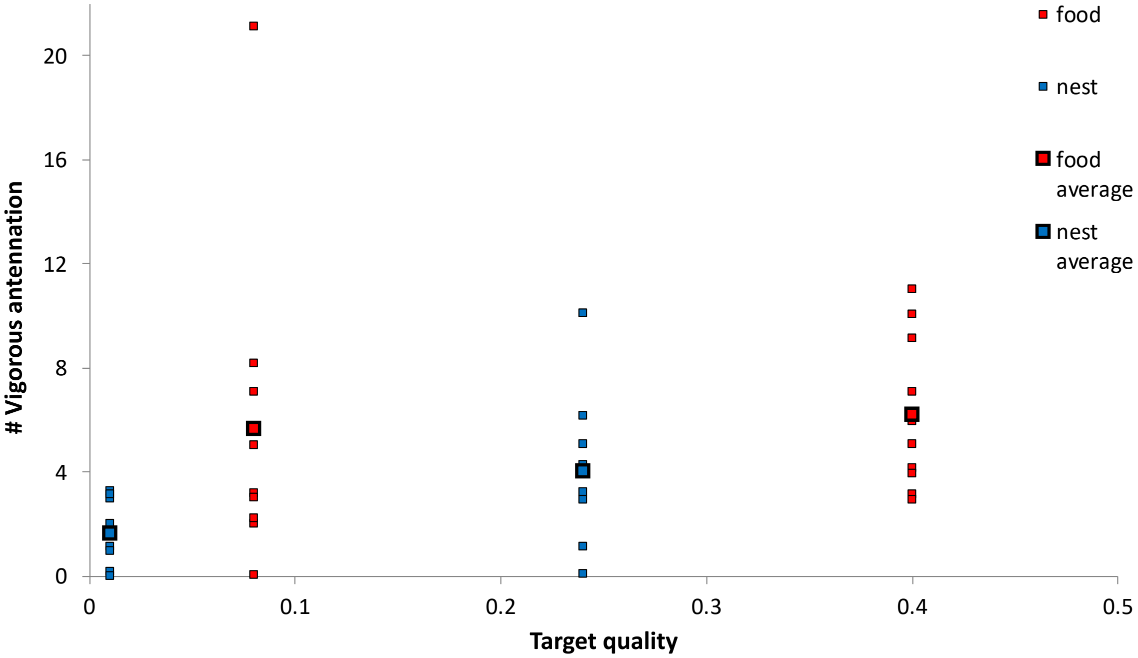


Fig. 2.6. Comparison of behavior by recipients of shaking and controls, see Appendix A: Online Resource 8 for details on statistical tests. A) Duration of trophallaxis. B) Duration of staying in the entrance tunnel. The thick middle line indicates the median, while the upper hinge indicates 75th quantile, and the upper whisker indicates the largest value within 1.5 times the interquartile range above 75th quantile (Wickham 2009; Baptiste 2016).

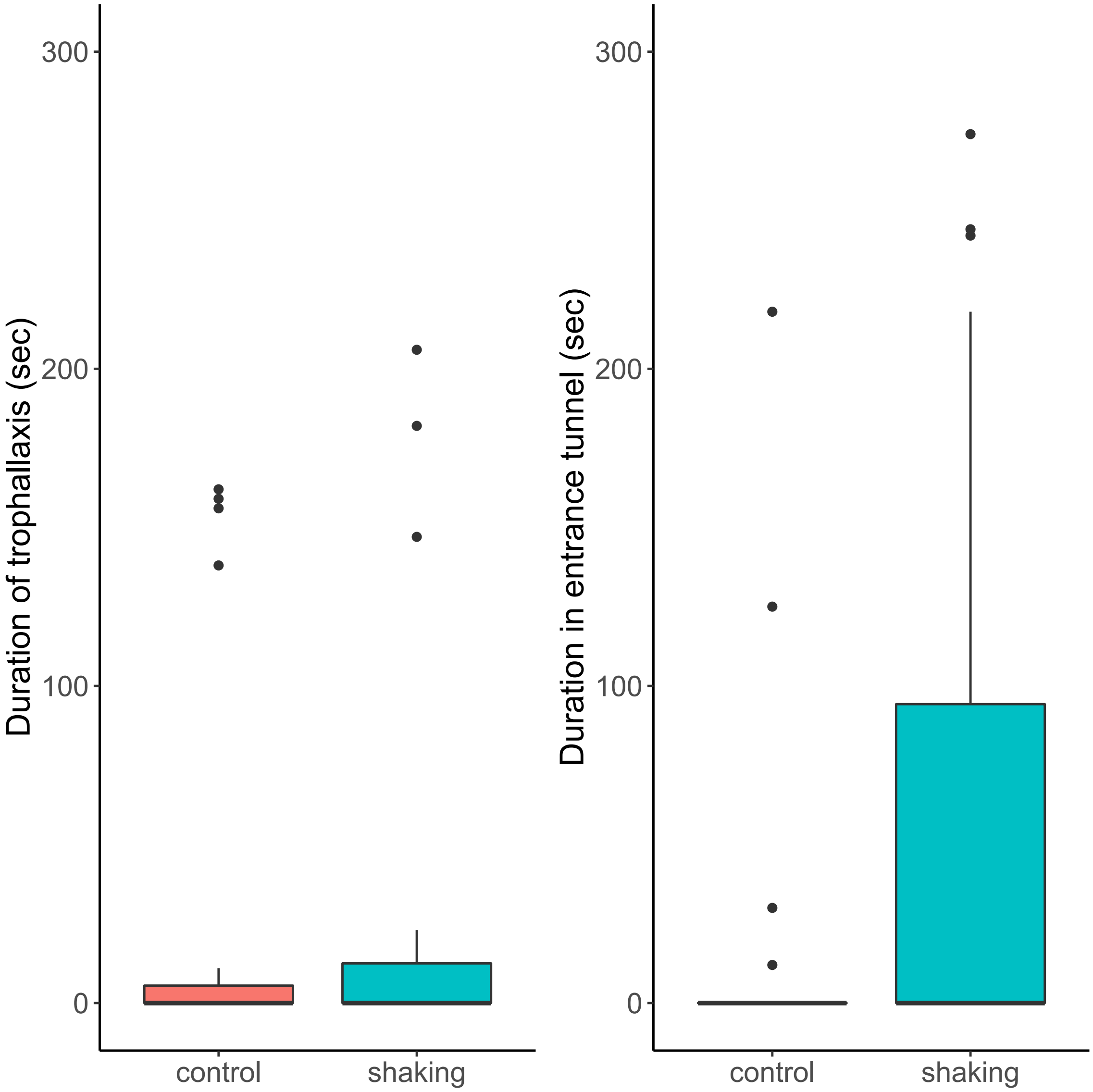


Table 2.1. Recipients of shaking vs. controls in the four behaviors

Behavior	Food quality	Recipients, n/N[†] (%)	vs.	Controls, n/N (%)	P-value, CMH[a]
Trophallaxis	Poor food	3/8 (37.5)		1/6 (16.7)	0.33
	Good food	7/14 (50)		4/13 (30.8)	
Move to the entrance	Poor food	3/8 (37.5)		2/6 (33.3)	0.33
	Good food	6/14 (42.9)		2/13 (15.4)	
Exit nest	Poor food	0/8 (0)		2/6 (33.3)	0.85
	Good food	1/14 (7.1)		0/13 (0)	
Follow a tandem run	Poor food	0/8 (0)		0/6 (0)	NA
	Good food	0/14 (0)		0/13 (0)	

[†] n/N indicates the number of ants engaged in a behavior divided by the total number of ants.

a. CMH = Cochran-Mantel-Haenszel X^2 test, testing for difference between recipients and controls, while controlling for food quality.

Table 2.2. Recipients of vigorous antennations vs. controls in the four behaviors

Behavior	Target type	Recipients, n/N (%)	vs.	Controls, n/N (%)	P-value, CMH[a]
Trophallaxis	Food	20/35 (57.1)		8/15 (53.3)	0.89
	Nest	2/17 (11.8)		1/14 (7.1)	
Move to the entrance	Food	11/35 (31.4)		6/15 (40)	0.86
	Nest	11/17 (64.7)		9/14 (64.3)	
Exit nest	Food	4/35 (11.4)		5/15 (33.3)	0.34
	Nest	11/17 (64.7)		9/14 (64.3)	
Follow a tandem run	Food	1/35 (2.9)		4/15 (26.7)	0.36
	Nest	2/17 (11.8)		0/14 (0)	

a. Testing for difference between recipients and controls, while controlling for target type.

Table 2.3. Ants in food vs. nest in the four behaviors

Behavior	Ant type	Ants in food, n/N (%)	vs.	Ants in nest, n/N (%)	P-value, CMH[a]
Trophallaxis	Recipient of vigorous antennation	20/35 (57.1)		2/17 (11.8)	0.00014*
	Control of vigorous antennation	8/15 (53.3)		1/14 (7.1)	
Move to the entrance	Recipient of vigorous antennation	11/35 (31.4)		11/17 (64.7)	0.020*
	Control of vigorous antennation	6/15 (40)		9/14 (64.3)	
Exit nest	Recipient of vigorous antennation	4/35 (11.4)		11/17 (64.7)	0.00014*
	Control of vigorous antennation	5/15 (33.3)		9/14 (64.3)	
Follow a tandem run	Recipient of vigorous antennation	1/35 (2.9)		2/17 (11.8)	0.74
	Control of vigorous antennation	4/15 (26.7)		0/14 (0)	

a. CMH testing for difference between ants in food and ants in nest, while controlling for target type;

significance level *$p < 0.05$.

Table 2.4. Recipients in poor nest vs. good nest in the four behaviors

Behavior	Recipients of vigorous antennation in poor nest, n/N (%)	Recipients of vigorous antennation in good nest, n/N (%)	P-value, Fisher's exact test
Trophallaxis	1/7 (14.3)	1/10 (10)	1
Move to the entrance	5/7 (71.4)	6/10 (60)	1
Exit nest	5/7 (71.4)	6/10 (60)	1
Follow a tandem run	1/7 (14.3)	1/10 (10)	1

Table 2.5. The number of shaking and vigorous antennation received by pre-tandem followers (*N* = 19).

Behavior and type of initiator to recipient	# of shaking or vigorous antennations total	
	Poor food	Good food
Shaking by TR leader	0	1
Vigorous antennation by TR leader	2	3

Table 2.6. The number of pre-tandem followers (*N* = 19) that received shaking, and those that received vigorous antennation.

Behavior and type of initiator to recipient	# ants that received shaking or vigorous antennations	
	Poor food	Good food
Shaking by TR leader	0	1
Vigorous antennation by TR leader	1	2

Table 2.7. Pre-tandem followers vs. recipients of shaking in the four behaviors

Behavior	Food quality	Pre-tandem followers, n/N (%)	vs.	Recipients of shaking, n/N (%)	P-value, CMH[a]
Trophallaxis	Poor food	4/9 (44.4)		3/8 (37.5)	0.32
	Good food	1/10 (10)		7/14 (50)	
Move to the entrance	Poor food	8/9 (88.9)		3/8 (37.5)	0.041*
	Good food	7/10 (70)		6/14 (42.9)	
Exit nest	Poor food	4/9 (44.4)		0/8 (0)	0.035*
	Good food	3/10 (30)		1/14 (7.1)	
Follow a tandem run	Poor food	9/9 (100)		0/8 (0)	3.0×10^{-9}*
	Good food	10/10 (100)		0/14 (0)	

a. CMH testing for difference between pre-tandem followers and recipients of shaking, while controlling for food quality; significance level *$p < 0.05$.

CHAPTER 3

FOOD VERSUS SAFETY: THE QUESTION FOR THE ANTS

Abstract

Animals often face a tradeoff between obtaining food and protecting themselves from predators or other risks that accompany foraging. In eusocial insects, this tradeoff requires adaptive allocation of workers to competing tasks, often mediated by recruitment communication. No study so far simultaneously posed foraging and nest selection challenges and tested for tradeoffs in worker allocation to each task. I hypothesized that colonies of the ant *Temnothorax rugatulus* face a tradeoff between foraging and protective tasks, and that they adaptively allocate workers to each task. I predict that colonies that face high hunger would allocate less effort to foraging when they also face high nest need, compared with when they have low nest need. Likewise, colonies that face high nest need would allocate less effort to nest-site selection when they also face high hunger, compared with when they face low hunger. I investigated this by varying the relative importance of foraging versus nest-site selection and observing whether and how colonies changed their investment in these tasks. Specifically, I manipulated their hunger state and the condition of their nest (i.e., shelter from potential predators, desiccation or extreme temperatures). I exposed colonies to all combinations of high and low hunger and complete and half removal of the nest roof (high and low nest need, respectively). For each combination, I simultaneously offered each colony a rich sucrose feeder and a high-quality new nest, and measured colony allocation to exploration, visitation and recruitment at each target. Results on the beginning of emigration show some evidence that the start time of emigration depends on hunger, in line with the tradeoff hypothesis:

there was no difference in emigration times based on nest need alone, but colonies disproportionately motivated to find a new nest (low hunger and high nest need) start emigrations earlier than colonies disproportionately motivated to find food (high hunger and low nest need). Relative worker allocation between food and nest shows that colonies that are disproportionately motivated to food allocate more to food compared to nest than colonies disproportionately motivated to find a nest, which is also in line with the tradeoff hypothesis. The rate of cumulative nest visits was higher for colonies with low hunger compared to those with high hunger, which again supports the tradeoff hypothesis. In sum, several of my results support the tradeoff hypothesis, and I discuss several possible mechanisms. This suggests that other social insects and other social groups could face this tradeoff as well, and if so, it will be interesting to investigate how they do so.

Introduction

Tradeoffs are relevant to many aspects of animal biology (Davies et al. 2012) and played a crucial role in the development of life-history theory (Stearns 1989). For an animal to increase its fitness, it has to resolve many tradeoffs, such as investment in current versus future offspring (Pianka and Parker 1975; Bell 1980; Miles, Sinervo, and Frankino 2000), number of offspring versus each offspring's quality (Lack 1947), brighter color for mating advantage versus reduced risk of detection by predators (Endler 1980; 1983), and speed versus accuracy when making decisions (Heitz 2014). Some of these tradeoffs concern allocation of effort to competing tasks: avoiding predation risk versus reproductive activity (Burk 1982; Berglund and Rosenqvist 1986; Rodríguez-Muñoz, Bretman, and Tregenza 2011), avoiding predation risk versus foraging (Milinski and Heller 1978; Sih 1980; Werner et al. 1983; Lima and Dill 1990; Rayor and Uetz 1990). When faced with such tradeoffs between competing tasks, animals are hypothesized to allocate their effort or energy according to the relative importance of the tasks to increase fitness.

One tradeoff of importance is foraging for food versus remaining in protective shelter (Lima, Valone, and Caraco 1985). Shelter helps animals to avoid predators (Holbrook and Schmitt 2002; Forstmeier and Weiss 2004; Shochat et al. 2004; Mikát et al. 2019) or parasitoids (Orr, Seike, and Gilbert 1997; Folgarait and Gilbert 1999), or to maintain favorable microclimatic conditions such as humidity (Schwarzkopf and Alford 1996; Seebacher and Alford 2002), temperature (Cerdá, Retana, and Cros 1998), and light (Latty and Beekman 2010). A large part of the success of social insects is believed to be due to their nests, which provide improved microclimatic conditions and protection from predation (Seeley 1985; Hölldobler and Wilson 1990; Dornhaus et al. 2004).

In eusocial insect colonies, a tradeoff requires adaptive allocation of workers between competing tasks or targets. For example, some workers in a colony explore their surroundings while others exploit a found resource (Mosqueiro et al. 2017; Cook et al. 2018), foraging for water versus nectar (Lindauer 1961), foraging for pollen versus nectar (Page et al. 2006), or foraging among multiple food sources (Beckers et al. 1990; Seeley, Camazine, and Sneyd 1991). These decisions are often mediated by recruitment communication, which brings nestmates to a place where work is required (E. O. Wilson 1971), by increasing worker traffic to a more favorable resource (Beckers et al. 1990; Seeley, Camazine, and Sneyd 1991; Pratt and Sumpter 2006; Sasaki and Pratt 2013).

It is not yet known whether foraging versus finding a shelter represents a tradeoff for social insect colonies, and if so, how they respond to the tradeoff. The study that came closest to answering this question dealt with nest maintenance instead of finding a nest: When foraging is interrupted by a plastic barrier, *Pogonomyrmex barbatus* harvester ants respond with less foraging activity and more nest maintenance activity, showing that the colony balances its workforce between foraging and keeping the nest and entrance area clear of debris (Gordon 1986). Other studies have dealt with foraging versus predation risk in social insects, but predation risk in these cases affected the individual foragers outside the nest rather than the colony itself (Cartar 1991; Korb and Linsenmair 2002): the forager weighing the relative value of feeding versus avoiding its predation is a distinct problem from the colony weighing the relative value of foraging through workers versus avoiding colony-scale predation. But no study simultaneously posed foraging and nest selection challenges and tested for tradeoffs in worker allocation to each task.

Temnothorax rugatulus is a good system to study this question for two reasons. First, *Temnothorax* is one of two model organisms for house hunting, along with honeybees (Dornhaus et al. 2004; Beekman and Dussutour 2009; Pratt 2010; Seeley 2010). It has also been studied during foraging (Gottlieb et al. 2013; Shaffer, Sasaki, and Pratt 2013) and recruits readily in both situations in the lab. Second, it is better suited to address this question than the honeybees, because unlike bees which emigrate and forage in separate stages (Tanner and Visscher 2006; Seeley 2010), *Temnothorax* ants can emigrate from an intact nest (Dornhaus et al. 2004), and thus may need to simultaneously perform both activities. A previous study showed that *Temnothorax rugatulus* does prefer to move to new nests in areas that previously had food, but that study featured two options for a new nest that had identical quality, so this did not pose a tradeoff between food and nest (Cao and Dornhaus 2011).

I studied colony recruiting for both food and nest tasks. I hypothesized that colonies of the ant *T. rugatulus* face a tradeoff between foraging and protective tasks, and that they will respond adaptively, allocating their workers to each task in a fitness-increasing way (the tradeoff hypothesis).

When colony-level motivation for finding food is high, the colony will allocate more workers to food. But because a colony's workforce is limited, I predicted that colony-level motivation for finding a new home will also affect the colony's recruitment response to food, and vice versa. For example, if colony-level motivation for a new home is high, the colony will allocate less resources to food and more to the nest, relative to when it has low motivation to find a new home.

I investigated this hypothesis and predictions by varying the relative need for food versus need for finding a shelter and then observing whether and how colonies changed their investment in these tasks. Specifically, I manipulated their hunger state, which affects their recruitment rate regarding food (Gottlieb et al. 2013; Shaffer 2014), and the condition of their nest, which affects the speed of emigration mediated by recruitment to find a new nest (Dornhaus et al. 2004; Pratt and Sumpter 2006). I exposed colonies to all four combinations of high and low hunger and high and low nest need. By creating a large enough competition between the colony's need for food and a new nest, I assumed that I created a tradeoff between food and nest needs. For each combination, I simultaneously offered each colony a rich sucrose feeder and a high-quality new nest, and I measured the colonies' allocation of recruitment, visitation at each target as well as exploration.

If there is no tradeoff between the two resource types, then I expected that recruitment and visitation to a resource would be only dependent on the colony state for that resource (e.g., if colony state for food is low hunger, food recruitment should be low regardless of whether the colony state regarding need for a new nest is high or low). But if food and nest needs represent a tradeoff for the colony, then the colony state for a new nest should affect the recruitment response for food. Likewise, the colony state for food should affect the recruitment response regarding a new nest.

Methods

Subjects

I collected *T. rugatulus* colonies from the Pinal Mountains in Arizona (N 33° 19.00’ W 110° 52.56’). I used 40 colonies in this experiment; these colonies were collected in May 2016 and February 2017. The experiments were done in June 2017. All colonies had one queen, except for one colony in low hunger and low nest need treatment. Worker populations ranged between 25 and 400, and brood populations ranged between 25 and 200. I maintained colonies as described in Sasaki et al. (2015), feeding them an agar-based diet (Bhatkar and Whitcomb 1970). For most of the year, colonies were housed on laboratory benches or in a diurnal incubator at a 14:10 L:D schedule, at approximately 22 °C and 15 °C (light and dark periods, respectively). Ten colonies (collected in May 2016) were overwintered for several weeks in a refrigerator at 5 to 15 °C, to simulate winter conditions in the field, then returned to normal conditions several months before the experiments. But 30 colonies collected in February 2017 were not overwintered.

Treatments

To test whether colonies face a tradeoff between foraging and emigration and whether colonies respond adaptively to the tradeoff, I simultaneously manipulated colony-level motivation for food and emigrating to a new home.

I had four manipulation treatments, with 10 colonies per treatment. Each colony was used for only one trial during these experiments:

1. Low food (*f*) need, low nest (*n*) need (*fn*)
2. Low food need, high nest (*N*) need (*fN*)

3. High food (*F*) need, low nest need (*Fn*)
4. High food need, high nest need (*FN*)

The logic of these treatments was that if the colonies face a tradeoff between foraging and emigration and respond adaptively to the tradeoff, then nest need will affect food allocation, and food need will affect nest allocation. Specifically, I first predict that *fn* colonies should allocate more workers to food than *fN* colonies. This is because *fn* colonies face less competition from nest need than *fN* colonies, even though the two treatments have the same food need. I predicted food allocations will be higher for *Fn* than *FN* based on the same logic. As for *fn* and *FN*, I am not sure which one would have a higher allocation under the tradeoff hypothesis, because the two needs are at a similar level in both treatments.

For nest allocations, I predicted *fn* colonies will allocate more workers to nest tasks than *Fn* colonies. This is because *fn* colonies face less competition from food need than *Fn* colonies, even though the two treatments have the same nest need. I predicted nest allocations will be higher for *fN* colonies than *FN* colonies based on the same logic. To create the four treatments, I had two manipulation types for food and two manipulation types for nest.

Low food need. I starved colonies by depriving them of the agar-based diet (Bhatkar and Whitcomb 1970) for about a day (21 hours) before the experiments.

High food need. I starved colonies by depriving them of the agar-based diet for 15 days before the experiments. Gottlieb et al. (2013) and Shaffer (2014) showed that colonies do more exploration, visitation and recruitment to the food target after starvation.

Before manipulation, the home nest consisted of a 2.4 mm-thick balsa wood slat between two glass microscope slides (50 X 75 mm), with a circular cavity at 40 mm in diameter and a ~2 mm wide entrance tunnel. About 2 hours before the experiment, I cut the tapes that held the glass slides and balsa slat together to facilitate moving the top glass slide. About 10 min before starting the experiments, I moved the top glass slide (the roof):

Low nest need. I slid the roof of the home nests halfway off (Fig. 3.1).

High nest need. I removed the entire roof of the original nests. Dornhaus et al. (2004) and Pratt and Sumpter (2006) showed that colonies emigrate earlier to a new nest when the nest roof is removed, compared to colonies in intact nests.

I subjected each of the 40 colonies to an experimental trial, as follows. I placed a colony in its nest in a 50 x 50 cm arena (Fig. 3.1) and left it to acclimate for ~2 hours. About 10 min before starting a trial, I moved the roof of the colony to manipulate its nest need. I introduced a glass depression slide (feeder), then introduced the new nest (Fig. 3.1 and Fig. 3.2). Then I put 0.1 ml of sucrose solution (1.0 M) in the feeder. I pseudorandomized (by treatment) whether the feeder was on the left side of the home nest (and the new nest on the right side) or vice versa. I recorded these experiments using a SONY FDR-AX53 camera, at 4K resolution, providing an overview of the arena. In another 50 x 50 cm arena next to the arena above, I simultaneously ran another trial using the same approach, with another SONY FDR-AX53 camera. I pseudorandomized (by treatment) whether each trial was run in the left or right arena. Each colony had at least two weeks since their previous emigration to minimize the influence of colony memory on current trials (Langridge, Franks, and Sendova-Franks 2004). I recorded each trial for two hours and 30 min.

To test my predictions on worker allocation by colonies, I measured recruitment events, the number of target visitation, and arena exploration from these recordings as described below.

Recruitment latencies

To see how long it takes for colonies to start tandem running to food, I recorded the first instance of a tandem leader reaching the feeder for each colony. To test for differences among treatments in the latency until the first tandem run, I performed survival analysis using the Cox proportional hazard model (Andersen and Gill 1982; Therneau and Grambsch 2000; Therneau 2015). When I found a significant effect of treatment, I ran Tukey's post hoc test using the glht() function (Hothorn, Bretz, and Westfall 2008; Mizumoto, Fuchikawa, and Matsuura 2017) to test the difference between each treatment. Under the tradeoff hypothesis, I predicted that the latency until the first food tandem run will be smaller in *Fn* colonies than *FN* colonies, as well as in *fn* colonies than *fN* colonies. In other words, latency will not only depend on food need, but it will be smaller in low nest need (LN) colonies than high nest need (HN) colonies.

To see how long it takes for colonies to start tandem running to nest, I recorded the first instance of a tandem leader entering the new nest for each colony. To test for differences among treatments in the latency until the first tandem run, I performed survival analysis using the Cox proportional hazard model, in the same way as described above. Under the tradeoff hypothesis, I predicted that the latency until the first nest tandem run will be smaller in *fN* colonies than *FN* colonies, as well as in *fn* colonies than

Fn colonies. In other words, latency will not only depend on nest need, but it will be smaller in low food need (LF) colonies than high food need (HF) colonies.

To see how long it takes for colonies to start emigrating to the new nest, I recorded the first instance of a transporting ant entering the new nest for each colony. A transporter carrying another ant to a new nest shows that the ant is committed to that nest (Pratt et al. 2005), as well as the colony (Sasaki et al. 2015). To test for differences among treatments in the latency until the beginning of transports, I performed survival analysis using the Cox proportional hazard model, in the same way as described above. Under the tradeoff hypothesis, I predicted the same pattern in latency to transport as in latency to nest tandem run above: it will be smaller in low food need (LF) colonies than high food need (HF) colonies.

The number of recruitment acts

To see how much tandem recruitment colonies allocate to food, I measured the number of tandem leaders arriving at the feeder, after monitoring the home nest to record tandem runs beginning at the home nest. To test the effects of nest treatment on food tandem runs, I used the analysis of covariance (ANCOVA; Faraway 2004) to model the effect of predictor variables on the number of food tandem runs, which is the dependent variable. The predictor variables with the full model (Whittingham et al. 2006) are: food treatment, nest treatment and time, and then their interaction terms: food treatment × time, nest treatment × time, food treatment × nest treatment, and food treatment × nest treatment × time. The predictor of interest for the tradeoff hypothesis is nest treatment × time, which is the effect of nest treatment on the rate of food tandem runs, or the number of food tandem runs over time. Under the tradeoff hypothesis, I predict that LN colonies will have a greater rate of increase in the number of food tandem runs than HN colonies. I used the cumulative number of food tandem runs as the dependent variable above to detect the amount of increase throughout the trial period, including the total value in the last time interval. I did not consider the main effects as important in ANCOVA models except for ANCOVA in exploration. This is because these effects indicate the difference in intercepts, and I did not measure anything at time 0, except for exploration.

To see how much tandem recruitment colonies allocate to nest, I measured the number of tandem leaders entering the new nest. To test the effects of food treatment on nest tandem runs, I used ANCOVA to model the effect of predictor variables (which are the same as above) on the number of nest tandem runs, which is the dependent variable. The predictor of interest for the tradeoff hypothesis is food treatment × time, which is the effect of food treatment on the rate of nest tandem runs. Under the tradeoff hypothesis, I predict that LF colonies will have a greater rate of increase in the number of nest tandem runs than HF colonies. I used the cumulative number of nest tandem runs as the dependent variable above to detect the amount of increase over the trial period, including the total value in the last time interval.

When the model residuals appeared non-normal in the ANCOVA models above, I used log transformation or square-root transformation on the dependent variable to achieve residuals that better fit the ANCOVA assumptions.

Visitation

To see how many workers colonies allocate to visit food, I measured the number of ants drinking at the feeder. I made counts at the feeder every 10 min. To test the effects of nest treatment on food visits, I used ANCOVA to model the effect of predictor variables (which are the same as above) on the number of food visits, which is the dependent variable. The predictor of interest for the tradeoff hypothesis is nest treatment × time, which is the effect of nest treatment on the rate of food visits. Under the tradeoff hypothesis, I predict that LN colonies will have a greater rate of increase in the number of food visits than HN colonies. I used the cumulative number of food visits as the dependent variable above to detect the amount of increase over the trial period, including the total value in the last time interval.

To see how many workers colonies allocate to visit the new nest, I measured the number of ants that are in the new nest: I counted all entries and exits through the new nest entrance, then calculated a net value of entry every 10 min, and accumulated this value to detect the amount of increase over the trial period. To test the effects of food treatment on nest visits, I used ANCOVA to model the effect of predictor variables (which are the same as above) on the number of nest visits, which is the dependent variable. The predictor of interest for the tradeoff hypothesis is food treatment × time, which is the effect of food treatment on the rate of nest visits. Under the tradeoff hypothesis, I predict that LF colonies will have a greater rate of increase in the number of nest visits than HF colonies.

Exploration

To see how much exploration each colony does, I counted the number of ants that were in the arena floor. I counted the number every 10 min, excluding any ant that was stepping on either of the two targets or the home nest. I used ANCOVA here as well, with exploration as the dependent variable. I expect that exploration will depend on the overall motivation state of the colony, so I predict that *FN* colonies will have the highest exploration, then *Fn* or *fN* colonies (which comes first depends on whether the colonies treat HF as more urgent or HN as more urgent), then *fn* colonies will have the lowest exploration. I also expect that exploration in the first 30 min of trial will be higher than the second 30 min, because colony motivation will likely decrease as ants exploit the feeder and start recruiting to the new nest. I did not use cumulative values for exploration, because I wanted to see how much exploration colonies did at any given moment, rather than overall values.

Differential recruitment

To see how each colony allocates its recruitment to food versus nest, I measured differential recruitment (food tandem runs minus nest recruitment for each colony). I calculated this measure every 10 min, without accumulating these values over time. With this measure, I can measure relative allocation between food and nest directly since the differential is taken for each colony, and accounts for the possible effect of colony size. I predicted that the differential recruitment will be highest for *Fn*, which is highly motivated for food but not for nest, then *FN* or *fn*, then finally *fN*, which is highly motivated for nest but not for food. To test for differences in response among treatments, I used the nonparametric Kruskal-Wallis test to measure the difference due to the treatments (the variances were homoscedastic, but the distributions were not normal with Shapiro-Wilk tests). When Kruskal-Wallis was significant, I ran Nemenyi posthoc test (Hollander and Wolfe 1999; Pohlert 2014), with corrected Chi-squared because of ties in ranks, to measure the differences between pairs of treatments.

Differential visitation

To see how each colony allocates its visitation between food and nest, I measured differential visitation (food visits minus nest visits for each colony). I calculated this measure every 10 min, without accumulating these values over time. With this measure, I can measure relative allocation between food and nest directly since the differential is taken for each colony, and accounts for the possible effect of colony size. I predicted that the differential visitation will be highest for *Fn*, which is highly motivated for food but not for nest, then *FN* or *fn*, then finally *fN*, which is highly motivated for nest but not for food. To test for differences between treatments, I used the nonparametric Kruskal-Wallis test to measure the difference due to the treatments (the variances were homoscedastic, but the distributions were not normal with Shapiro-Wilk tests). When Kruskal-Wallis was significant, I ran Nemenyi posthoc test, with corrected Chi-squared because of ties in ranks, to measure the differences between pairs of treatments.

For these variables, I decided to confine my observations to the first hour after camera start (i.e., one hour after introducing sugar water to the feeder), because the manipulated difference in state was maximized in the first hour. That is, the difference between high motivation and low motivation level was highest in the first hour, because as colonies exploit the feeder and recruit to the new nest, the decrease in motivation will be greater for high motivation colonies: For nest allocation, many transports started before the 1-hour mark in this experiment, and for food allocation, one in five colonies documented in Shaffer (2014) had significantly more food tandem runs in the first hour than those in the second hour. One exception is transport times, because in my experiments, nine colonies started transports after the 1-hour mark. I collected data until 150 min after the beginning of the experiment.

Other statistical analysis

I calculated all summary and inferential statistics using R, v. 3.5.1, to do all statistics (R Core Team 2018). More than one person, including JYC, coded the videos, so I tested whether the way each person coded was different: I took a 10-min sample per video from five videos for each treatment, totaling 20 videos across four treatments. I then calculated the intraclass correlation coefficient (ICC; Wolak, Fairbairn, and Paulsen 2012) for tandem runs across three observers, between one pair of observers, and between the other pair of observers. I used Cicchetti (1994)'s criteria to evaluate the similarity between observers. For tandem runs to food and tandem runs to nest, across three observers, ICC = 0.91. Between one pair of observers, ICC = 0.74, and between the other pair of observers, ICC = 0.98. All three of these values are considered good or better, according to Cicchetti (1994). I repeated this process for nest visits across two observers, using a summed value of nest visits over the 10-min period for each colony. For nest visits, across two observers, ICC = 0.63. This value is considered good according to Cicchetti (1994).

Results

When I provided each colony with a food target and a new nest target, all colonies across the four treatments discovered and visited the food at least once, and most colonies discovered and visited the new nest at least once (37 of 40 colonies; Table 3.1). Colonies showed more variation in their decision to recruit for the targets (Table 3.2): Both HF colonies (*Fn* and *FN*) started tandem running to the food, but only four *fn* colonies and five *fN* colonies started tandem running to the food. As for the new nest, four *Fn* colonies, six *FN* colonies, seven *fn* colonies, and seven *fN* colonies started tandem running to the new nest.

Recruitment latencies

Emigration to the new nest began when an ant started transporting another ant to the new nest. The *fN* colonies did not start transports significantly faster than *FN* colonies, and *fn* colonies did not start transports significantly faster than *Fn* colonies, either. This did not match my prediction under the tradeoff hypothesis. However, *fN* colonies, which I expected to have the highest nest allocation and start transporting the earliest under the tradeoff, started transports significantly faster than *Fn* colonies (Fig. 3.3; Cox proportional hazard model: $p = 0.007$, Tukey's post hoc test: $p = 0.007$ between *Fn* and *fN*). The comparisons between other pairs were not significant. The *fN* colonies allocated effort faster to the new nest compared to *Fn*. The fact that there is no difference between *fN* and *fn*, however, suggests that emigration time is not determined by nest treatment alone, but also by food treatment. Such effect of food treatment on emigration time is consistent with the tradeoff hypothesis and indirectly supports it.

The latency to tandem run for food was smaller in HF colonies than LF colonies, which is what I expect since HF colonies are more motivated to forage (Fig. 3.4; Cox proportional hazard model: $p < 0.001$). But the results do not match my prediction under the tradeoff hypothesis, because there was neither a difference between *Fn* and *FN* colonies, nor between *fn* and *fN* colonies (Fig. 3.4).

The latency to tandem run for nest was not different between treatments (Fig. 3.5; Cox proportional hazard model: $p < 0.54$), which does not match my prediction.

The number of recruitment acts

For the cumulative number of food tandem runs, this number increased faster with time when ants were hungrier (Fig. 3.6; the interaction between food treatment and time was significant ($p < 0.001$) and the direction was HF > LF in ANCOVA). This would be expected if food treatment affects the rate of food recruitment. There was no effect of nest treatment, though, which goes against my prediction under the tradeoff hypothesis.

For the cumulative number of nest tandem runs, the number increased faster when ants were hungrier ($p < 0.001$, Fig. 3.7). This opposes my prediction under the tradeoff hypothesis. This result would still be possible under the tradeoff hypothesis, if for LF lines, which have less competition from nest need, transports started sooner and tandem runs ended early. Indeed, significantly more *fN* colonies started transports than *Fn* (Fig. 3.3). However, when I considered the time of the first nest tandem runs, the four treatments did not differ significantly (Fig. 3.5).

Food visits

For the cumulative number of food visits, there was no effect of food or nest on the rate of food visits (Fig. 3.8; ANCOVA), and does not match my prediction under the tradeoff hypothesis, even though food visits did increase significantly with time ($p < 0.001$).

Nest visits

For the cumulative number of nest visits, the number increased significantly faster when ants were less hungry ($p = 0.010$, Fig. 3.9). This matches my prediction under the tradeoff hypothesis, because low food need (and less competition from food need) resulted in increased nest allocation.

Exploration

For the level of exploration, it decreased significantly as time passed (Fig. 3.10; $p < 0.001$ in ANCOVA), as expected. The rate of exploration was not significantly affected by any factor (Fig. 3.10), but I had positive raw data at 0 min, which means the intercepts do hold meaning for exploration. The HN colonies' exploration at 0 min was significantly higher than that of LN colonies (Fig. 3.10; $p = 0.015$), as expected. However, LF colonies' exploration at 0 min was significantly higher than that of HF colonies (Fig. 3.10; $p = 0.012$), which I did not expect.

Differential recruitments

For differential recruitments, I found that this value for *Fn* was significantly higher than *fN*, for 5/6 intervals I measured, but no other pairs were significantly different (Fig. 3.11; Kruskal-Wallis test: $p < 0.05$ for these intervals, and post hoc Nemenyi test was only significant between *Fn* and *fN* for these intervals). This does not match my prediction under the tradeoff hypothesis, because there was no difference between *Fn* and *FN* colonies, nor between *fn* and *fN* colonies. However, the fact that there is no difference between *Fn* and *fn* colonies suggests that recruitment allocation is not determined by food treatment alone, but by both treatments. Such effect of both treatment on recruitment allocation is consistent with the tradeoff hypothesis.

Differential visitation

For differential visitation, I found that this value for *Fn* was significantly higher than *fN*, for 3/6 intervals I measured, but no other pairs were significantly different (Fig. 3.12; Kruskal-Wallis test: $p < 0.05$ for these intervals, and post hoc Nemenyi test was only significant between *Fn* and *fN* for these intervals). This does not match my prediction under the tradeoff hypothesis, because there was no difference between *Fn* and *FN* colonies, nor between *fn* and *fN* colonies. However, the fact that there is no difference between *Fn* and *fn* colonies suggests that visitation allocation is not determined by nest food treatment alone, but by both treatments. Such effect of both treatment on visitation allocation is consistent with the tradeoff hypothesis.

Discussion

The experimental results are mixed in supporting the tradeoff hypothesis. The rate of cumulative nest visits was higher for LF colonies than HF colonies (for either level of nest motivation; Fig. 3.9), as predicted under the tradeoff hypothesis. This supports the hypothesis, because food treatment affected nest allocation for visitation as predicted. On the other hand, other variables I measured did not match my prediction under the tradeoff hypothesis, and did not support the hypothesis: the latency to food tandem run, the latency to nest tandem run, the latency to transport, the cumulative numbers of food tandem runs, of nest tandem runs and of food visits, as well as differential recruitment and differential visitation.

There are lines of evidence that indirectly support the tradeoff hypothesis. In latency to transport, *fN* colonies had significantly smaller latencies than *Fn* colonies, but there was no difference between *fN* and *fn* colonies (Fig. 3.3). I expect *fN* colonies to have a smaller latency than *fn* colonies if the latency is affected by nest treatment alone. This combined result suggests that emigration time is not determined by nest treatment alone, but also by food treatment. The effect of food treatment on emigration time is consistent with the tradeoff hypothesis. In the same reasoning, in differential recruitment and differential visitation, the only significant differences between treatments were between *fN* and *Fn* colonies (Fig. 3.11 and Fig. 3.12). However, these two findings provide less support than the latency to transport, because differential allocation included both food and nest components in the dependent variable. Hence, the observed pattern is expected whether food and nest needs affect allocation separately (i.e., food needs only affect food allocation and nest needs only affect nest allocation) or if the tradeoff hypothesis is true. But differential allocation shows that the significant effects I observed in food and nest allocation is not simply an effect of differences between colonies such as colony size, because the differential allocation was measured for each colony first, then compiled within each treatment.

A reason that the results are mixed in matching the prediction of the tradeoff hypothesis could be because the difference in nest need between LN and HN colonies is not great enough. In the latency to food tandem runs, HF lines have smaller latencies than LF lines showing a significant effect of hunger as expected, but *Fn* and *FN* colonies have similar latencies, as well as *fn* and *fN* colonies (Fig. 3.4). This result is expected if the tradeoff hypothesis is not true, but there are other indications that LN and HN colonies are not different enough in nest need: the latency to nest tandem runs is not significantly different between LN and HN colonies (Fig. 3.5; the four treatments were statistically indistinguishable). The latency to transport is not significantly different between *FN* and *Fn* colonies, nor between *fN* and *fn* colonies (Fig. 3.3). For cumulative number of nest tandem runs, nest treatment did not have a significant effect on the rate (Fig. 3.7). The rate of cumulative food tandem runs is greater for HF colonies than for LF colonies, again showing a significant effect of hunger, but nest treatment did not have a significant effect on the rate (Fig. 3.6).

Also, the explanation above that the difference in nest condition between HN and LN colonies is not great enough is supported by the overall order of the four treatments as predicted under the tradeoff hypothesis: in all of the figures except for the cumulative number of nest tandem runs (and excluding exploration), *fN* and *Fn* lines are in opposite extremes, while *FN* and *fn* lines sit more or less in the middle between *fN* and *Fn*. But these differences were often not statistically significant, as I discussed above.

Surprisingly for the cumulative number of nest tandem runs, HF lines had a significantly greater rate than LF lines, opposite of what I predicted. This could be because LF colonies start and switch to transports sooner than HF colonies, although the difference in the latency to start transport was not significant between LF and HF (Fig. 3.3).

Exploration

Regarding ants in the arena, the level of exploration decreased significantly with time (Fig. 3.10). Perhaps when food and nest needs are present at the beginning, ants rush out into the new arena to look for food or a new nest, but as time passes and ants find the desired targets, exploration decreases. It is possible that introducing a colony to the arena suddenly boosts exploration, but colonies had two hours to get used to the arena before food and nest targets were introduced.

Here, the intercepts do mean something, because I collected data at 0 min. As expected, HN colonies had significantly higher exploration than LN colonies at time 0, which suggests that colonies with high nest need explored the arena more to find a new nest. Because the roof was removed in the HN scenario, the ants might have been more likely to be outside the nest to begin with.

I expected HF colonies to have higher exploration than LF because the ants would be more motivated to find food (and more likely to find food via more exploration), but actually, LF colonies had significantly higher exploration than HF colonies at time 0, perhaps because HF colonies were saving energy due to food deprivation and exploring less, then spent more energy recruiting to a food source once it was found.

Also, *fn* was expected to have minimal exploration. Indeed, its exploration started low relative to other colonies, but declined at a slower rate than other treatments (although the differences were not statistically significant).

Implications

This research shows some evidence that colonies of *T. rugatulus* experience a tradeoff in allocation between foraging and emigration, supported by the cumulative number of nest visits, and indirectly by the latency to transport, differential recruitment and differential visitation. The results also show that exploration by colonies decreases over time as well.

This shows that colonies of social insects can face a tradeoff between food and nest tasks, similar to individual organisms. In my system, the tradeoff was partially evident in recruitment. It will be interesting to see whether other social insect colonies or other complex adaptive systems, such as amoeba colonies, fish schools, or a herd of wildebeest show this kind of tradeoff in allocation. I expect that more interest-united groups such as social insects will exhibit more of a tradeoff than in more amorphous groups such as a herd of wildebeest (especially if they are in a group based on the selfish herd effect; Hamilton 1971), because more sharing of resources is expected if a group has united interest. I expect individuals in a herd of wildebeest will try to find both food and shelter on their own. If interest-united groups show more of a tradeoff, then it will be interesting to see if more interest-united groups within social insects, such as a colony with one set of parents (monogamous ant, wasp, or termite colonies) show more of a tradeoff than social insects with more expected conflict among group members (colonies with one mother queen but multiple fathers or colonies with several queens, each with multiple partners). It will be also interesting to see if cohesiveness in general has an effect, or if colony size influences food–nest tradeoff in allocation. Perhaps in more amorphous groups, the pattern follows the ideal free distribution between food and nest tasks.

Mechanism: How does the colony allocate its workers between food and nest tasks?

Previous research (Chapter 2) showed that food recruiters and nest recruiters behave differently. This is a potential way that recruiters could convey the target type to the rest of the colony, a possible mechanism by which the colony could regulate the recruitment between two target types based on the colony state for each target type. Food and nest recruitment often differ in several species (Hölldobler 1971; Hölldobler, Möglich, and Maschwitz 1974; Hölldobler and Wilson 1978), so perhaps the recipients of these recruitment efforts can distinguish between food and nest recruitment, which makes it feasible that a colony assesses the options, or tradeoff between using food information or nest information. If recruits act on these differences, this would help the colony in allocating workers to different targets based on colony needs. Perhaps different ants have varying thresholds to respond to food stimuli versus nest stimuli, and this would decide how many ants a colony will allocate to food tasks. One such difference between food and nest recruiters is that food recruiters have a longer trophallaxis time in the nest, which makes their visit longer than those of nest recruiters (Chapter 2).

If there is a mechanism for the recruits to distinguish target type and result in colony-level response, this could facilitate similar investigations in other systems as well. For example, in honeybees, foragers switch more from sugar water to pollen when sugar concentration is lower (Arenas and Kohlmaier 2019). When colonies are offered low-quality sugar solution (a proxy for nectar) in-hive, the ratio of pollen to nectar foraging increases, and when colonies are offered high-quality sugar solution, the ratio of pollen to nectar foraging decreases (Arenas and Kohlmaier 2019).

Another possibility is that the colony has a common pool of recruits between food and nest tasks, as opposed to having different groups of workers dedicated to foraging and emigration, respectively (Pinter-Wollman et al. (2012) shows that ants engaged in emigration and foraging are often different ants, although there were some overlaps). My data show that exploration was mostly similar across treatments: there was no significant effect of food treatment or nest treatment on the rate of exploration, although the two nest treatments had a different starting point, as did the two food treatments (Fig. 3.10). The lack of differences in the rate of exploration, but that exploration decreases over time suggests that foraging and emigration have a common pool of workers. Indeed, in the ant *Tapinoma erraticum*, the foragers and brood transporters appear to come from a common pool of workers (Meudec and Lenoir 1982).

To measure relative allocation of recruitment between food and nest tasks, there could be other methods than counting all recruitment events as I did in this study, such as counting the number of recruitment events per recruiter. Some ants might be more persistent in recruitment than others. It is possible that nest recruiters are more persistent than food recruiters. Also, the number of recruitment events could be a factor of roundtrip time: If food recruitment takes longer before returning home, there might be fewer recruitment events per ant.

Conclusion

To conclude, I have found support for the tradeoff between food and nest through the cumulative number of nest visits, and indirectly through the latency to transport, differential recruitment, and differential visitation. I examined potential mechanisms such as recruits that can distinguish food recruiters from nest recruiters and having a common pool of workers for exploiting multiple resource types. This tradeoff and ensuing adaptive allocation will be interesting to find in other systems, to see how each system use its own mechanism to deal with the same issue in allocation between multiple resource types.

Table 3.1. Colonies visiting targets, first 60 min

Treatments	Colonies visiting food, n/N	Colonies visiting new nest, n/N
Fn	10/10	9/10
FN	10/10	8/10
fn	10/10	10/10
fN	10/10	10/10

Note. Tables show how many colonies ended up visiting the targets in the first 60 min. Total *N* = 40; 10 colonies per treatment.

Table 3.2. Colonies tandem running to targets, first 60 min

Treatments	Colonies tandem running to food, n/N	Colonies tandem running to new nest, n/N
Fn	10/10	4/10
FN	10/10	6/10
fn	4/10	7/10
fN	5/10	7/10

Note. Tables show how many colonies ended up recruiting to the targets in the first 60 min. Total *N* = 40; 10 colonies per treatment.

Fig. 3.1. Schematic representation of the arena setup. The new nest sits at one side of the arena while the feeder sits at the other side (left or right is pseudorandomized by treatment). Home nest has the roof half-removed to illustrate how I do this manipulation.

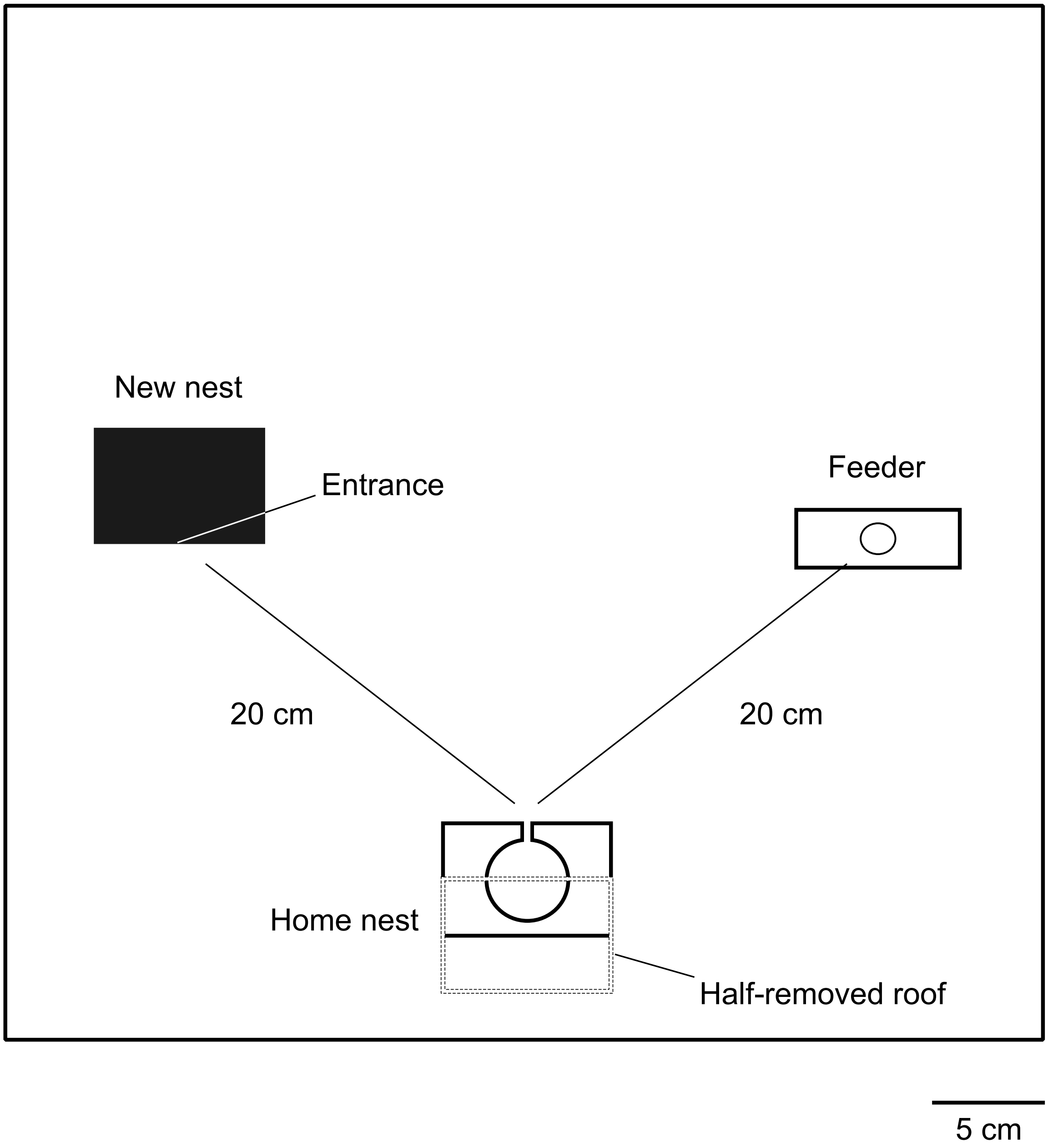


Fig. 3.2. 3D representation of the new nest design: entrance area = ~ 1.5 mm^2, cavity volume* = ~ 5.2 ml, light level in the nest = 4.99 lux. This figure was also used in Chapter 2 (TR information sharing).

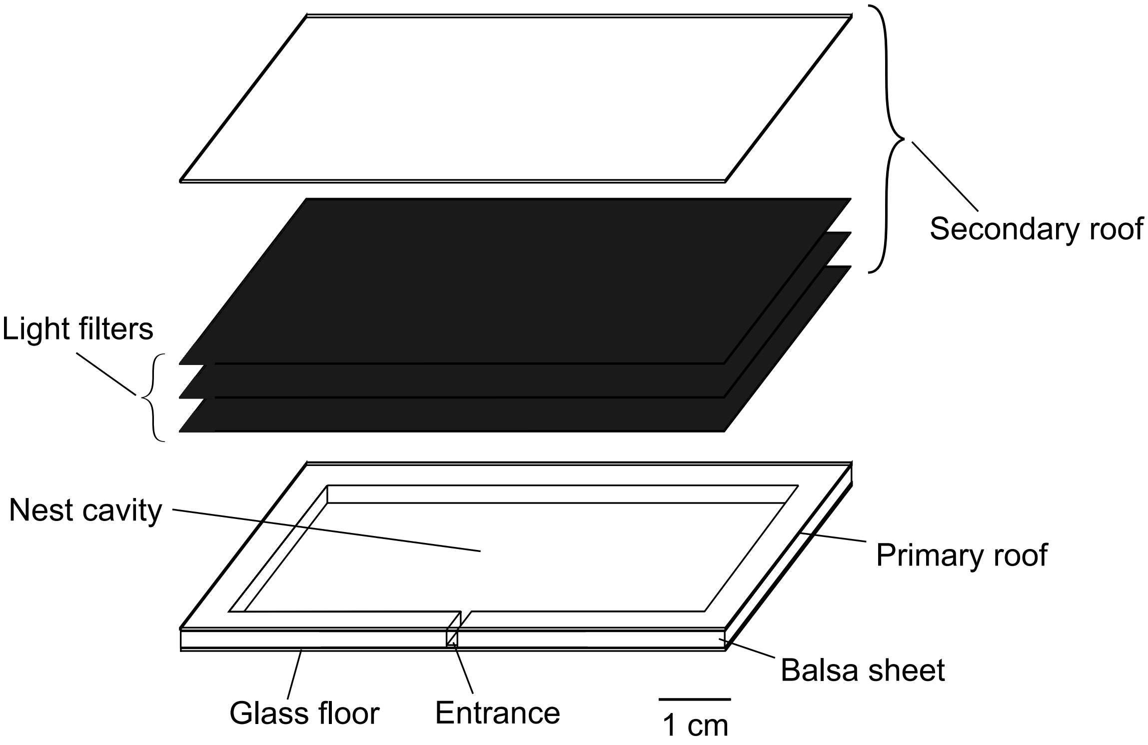


Fig. 3.3. Survival analysis of the proportion of colonies in pretransport. The lines show the number of colonies for each treatment still in pretransport, and the lines decline one step when a colony started transport. There was a significant difference between treatments (Cox proportional hazard model: $p = 0.007$). For the difference between each treatment, I ran Tukey's post hoc test: there was a significant difference between *Fn* and *fN* ($p = 0.007$). The comparison between five other pairs are not significant ($p > 0.05$). $N = 40$ colonies; 10 colonies per treatment. Data collected until 2 hours 30 min from experiment start time. Mean time for first transports: *Fn*: 113 min; *FN*: 85.7 min; *fn*: 72.8 min; *fN*: 45.9 min.

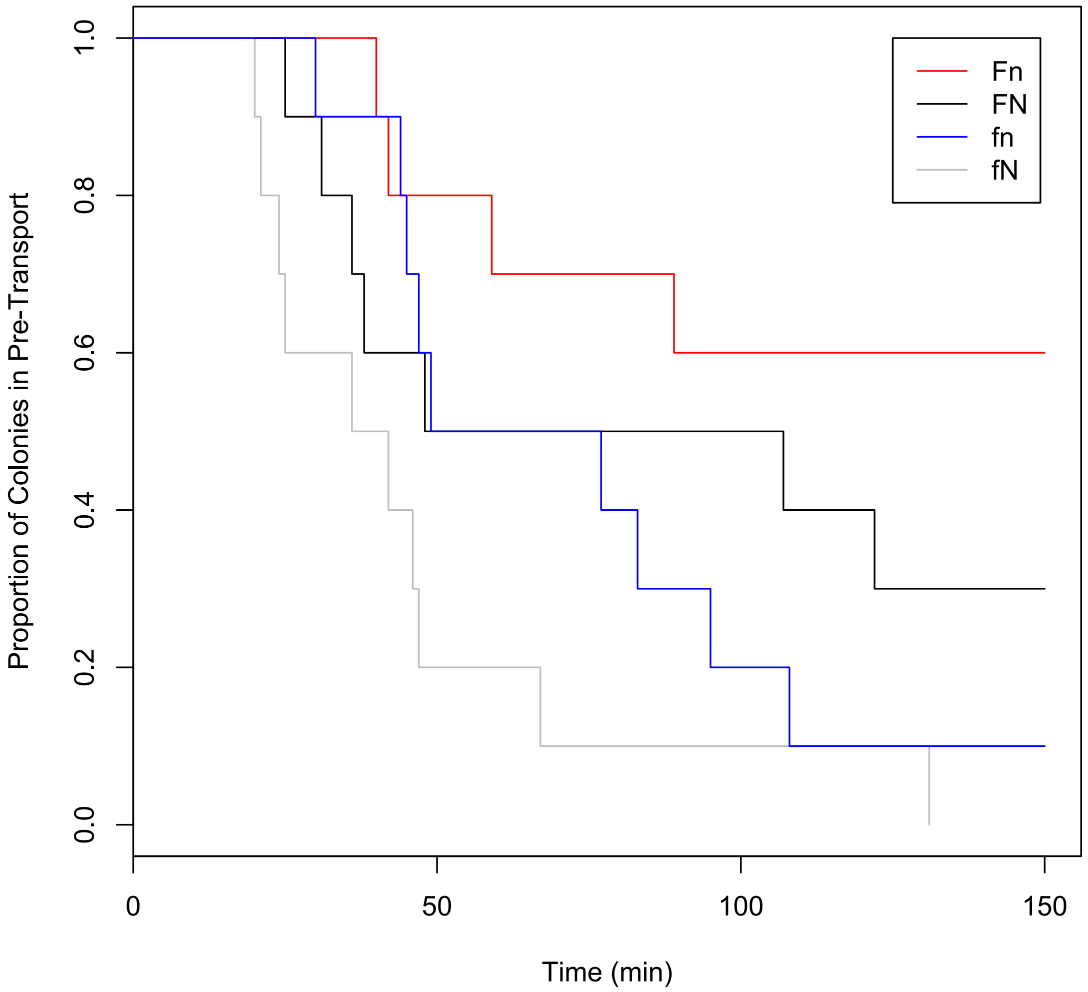


Fig. 3.4. Survival analysis of the proportion of colonies in prefood tandem run, or the proportion of colonies that did not yet start food tandem runs. The lines show the number of colonies for each treatment that were still prefood tandem run, and the lines decline one step when a colony started a food tandem run. According to a Cox proportional hazard model, there was a significant difference between treatments ($p < 0.001$). To test the difference between each treatment, I used Tukey's post hoc test: there was a significant difference between *Fn* and *fN* ($p < 0.001$), between *Fn* and *fn* ($p = 0.001$), between *FN* and *fN* ($p = 0.004$), and between *FN* and *fn* ($p = 0.004$). But there was no difference between *Fn* and *FN* ($p > 0.05$), and between *fn* and *fN* ($p > 0.05$). $N = 40$ colonies; 10 colonies per treatment.

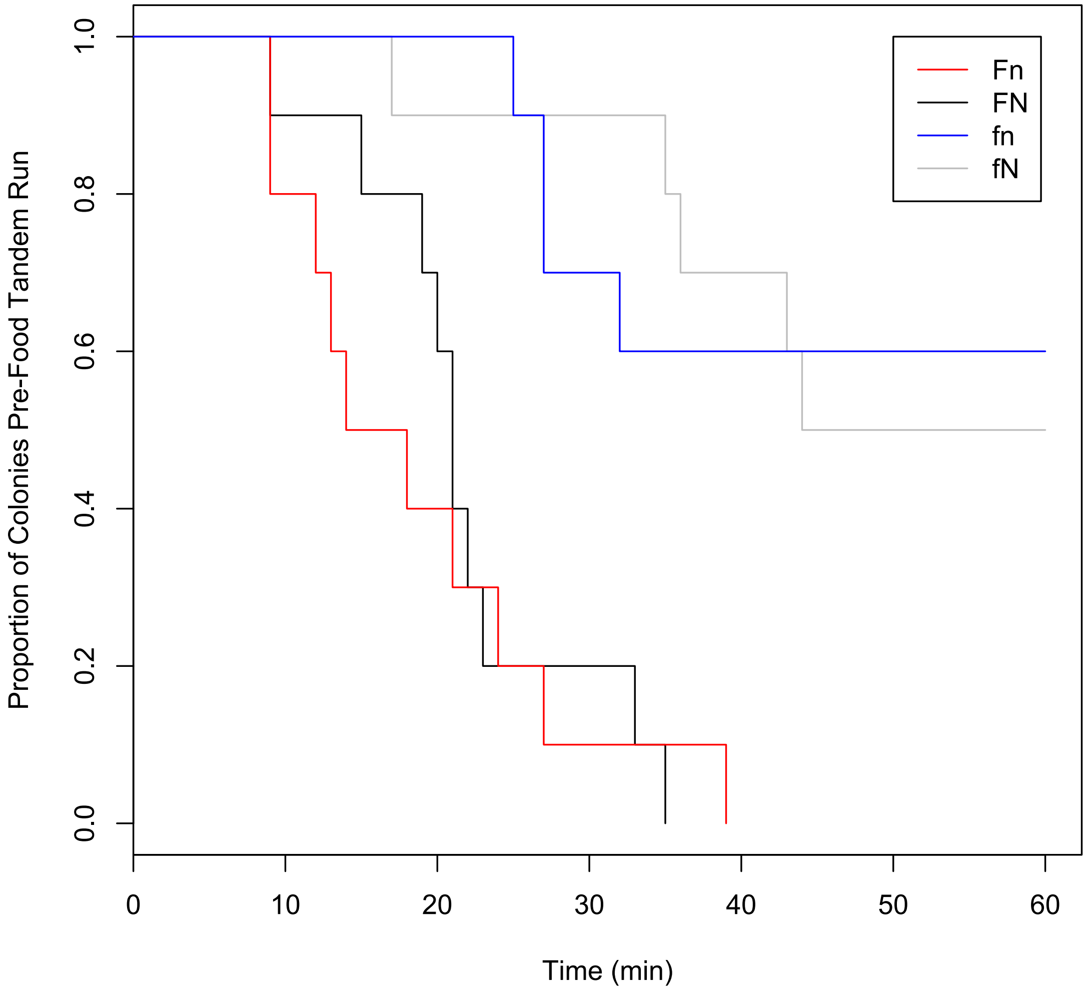


Fig. 3.5. Survival analysis of the proportion of colonies in prenest tandem run.
The lines show the number of colonies for each treatment that were still prenest tandem run, and the lines decline one step when a colony started a nest tandem run. According to a Cox proportional hazard model, there was no significant difference between treatments (p = 0.54). N = 40 colonies; 10 colonies per treatment.

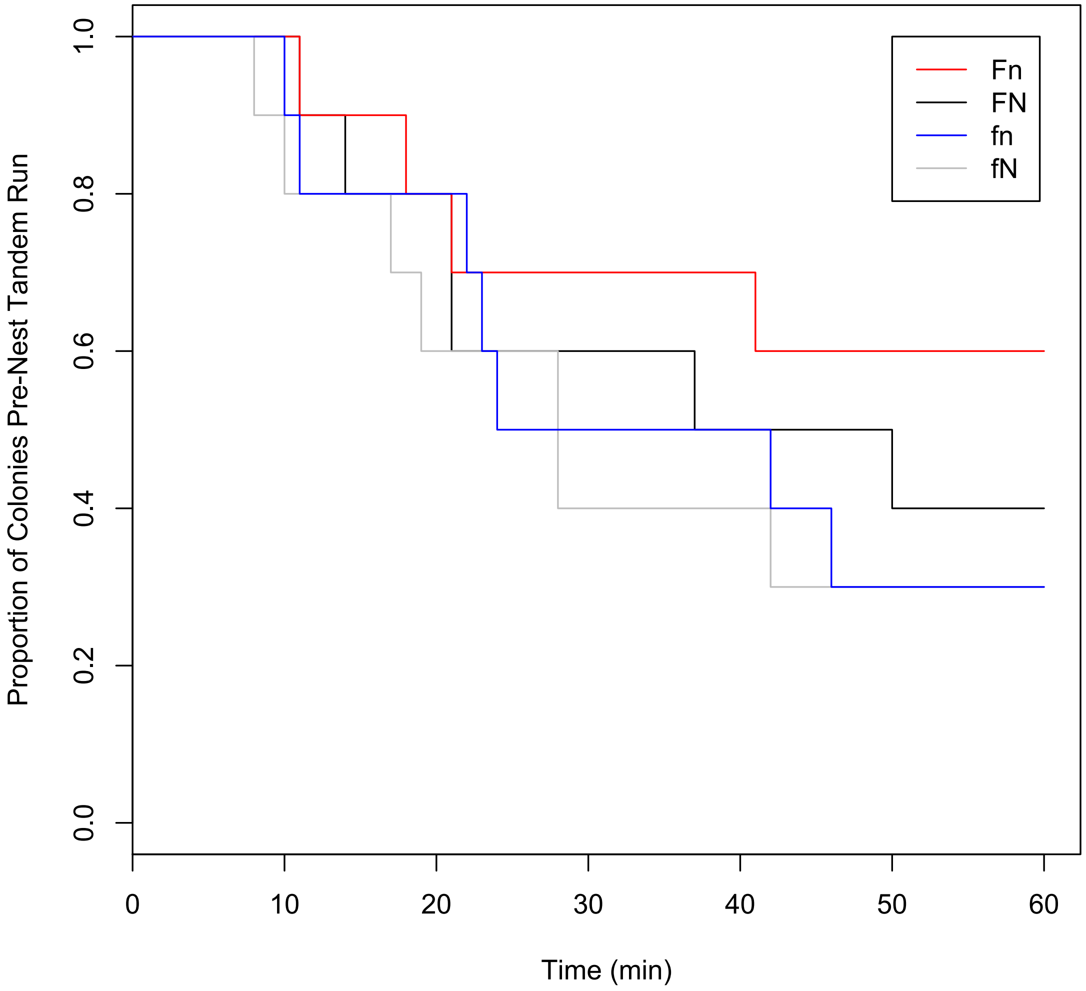


Fig. 3.6. The cumulative number of food tandem runs, first 60 min after experiment start, ± standard error. In the full ANCOVA model including interactions between model terms, the interaction between food treatment and time was significant ($p < 0.001$) and negative, indicating that when ants were hungrier, the cumulative number of food tandem runs increased faster (HF lines have higher slopes than LF). The effect of time was significant ($p < 0.001$) and positive, which means that the cumulative number of food tandem runs increased with time. Regarding the intercept, the effect of food treatment was significant ($p < 0.001$) and positive, which means LF > HF, because the intercept is at time 0.

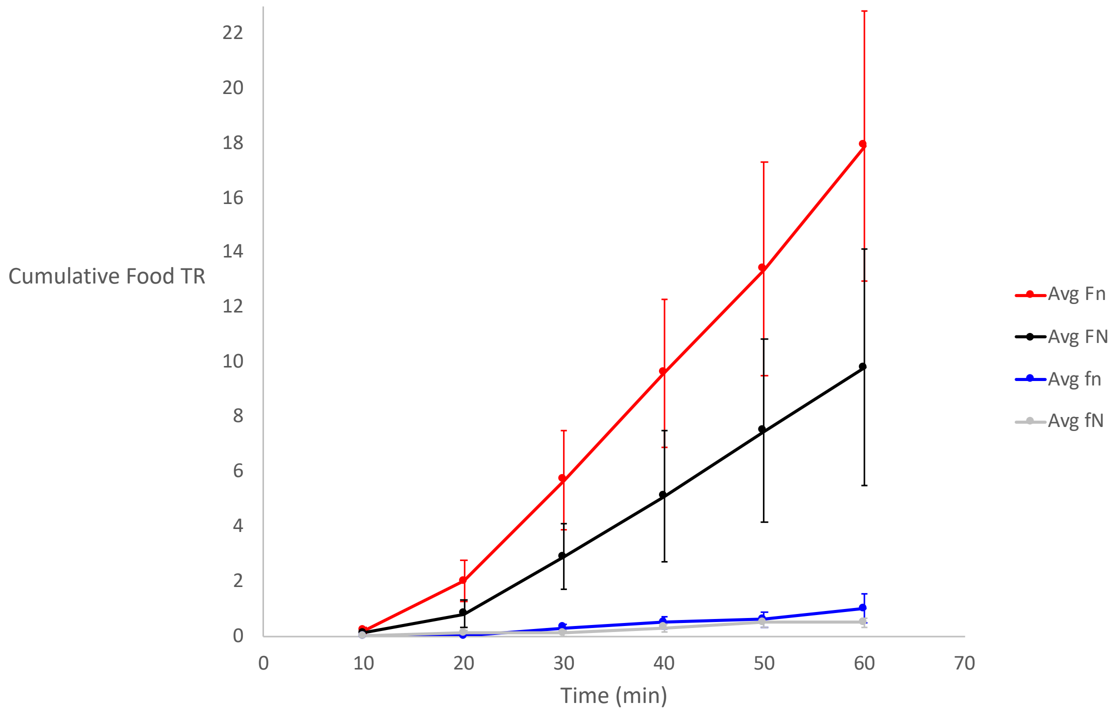


Fig. 3.7. The cumulative number of nest tandem runs, first 60 min after experiment start, ± standard error. In the full ANCOVA model (square-root transformed) including interactions between model terms, the interaction between food treatment and time was significant ($p < 0.001$) and negative, which means that when ants were hungrier, the cumulative number of nest tandem runs increased faster (higher slopes for HF lines than LF lines). The effect of time was significant ($p < 0.001$) and positive, which means that the cumulative number of nest tandem runs increased with time. Regarding intercepts, the effect of nest treatment was significant ($p = 0.002$) and negative, which means HN > LN. The effect of food treatment was significant ($p = 0.002$) and positive, which means LF > HF.

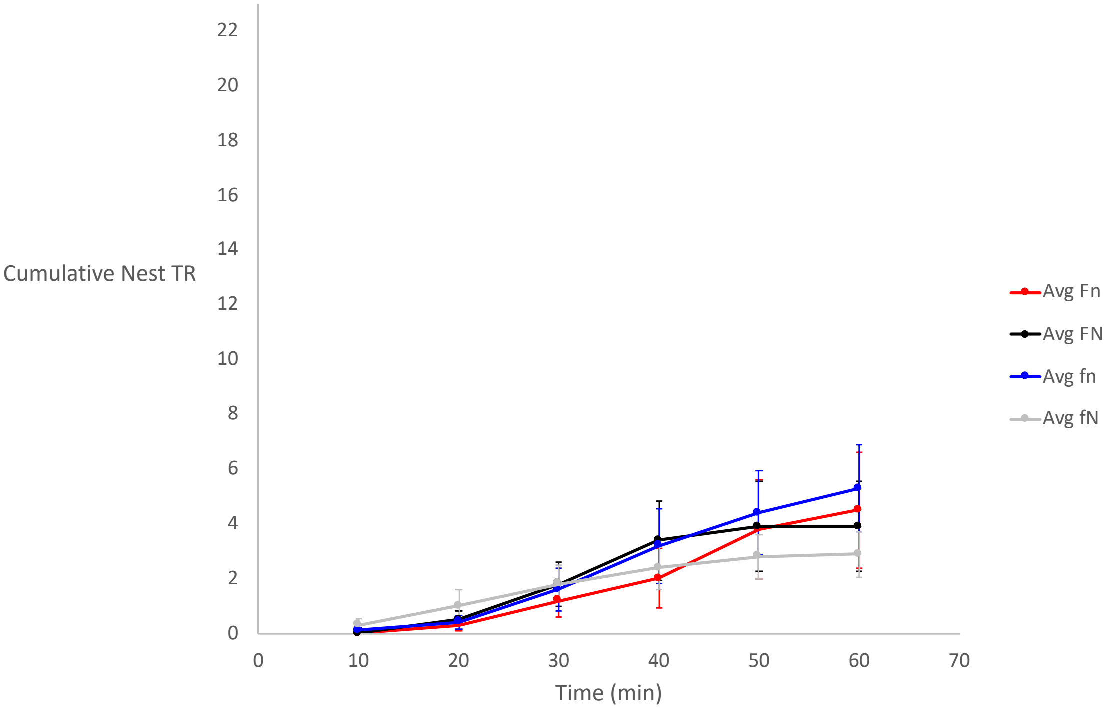


Fig. 3.8. The cumulative number of food visits, first 60 min after experiment start, ± standard error. In the full ANCOVA model (log transformed) including interactions between model terms, the interaction terms were not significant, which means that the treatments did not differ in slope or rate of food visits over time. The effect of time was significant ($p < 0.001$) and positive, which means that the cumulative number of food visits increased with time. Regarding intercepts, the effect of food treatment was significant ($p = 0.039$) and positive, which means LF > HF, because the intercept is at time 0.

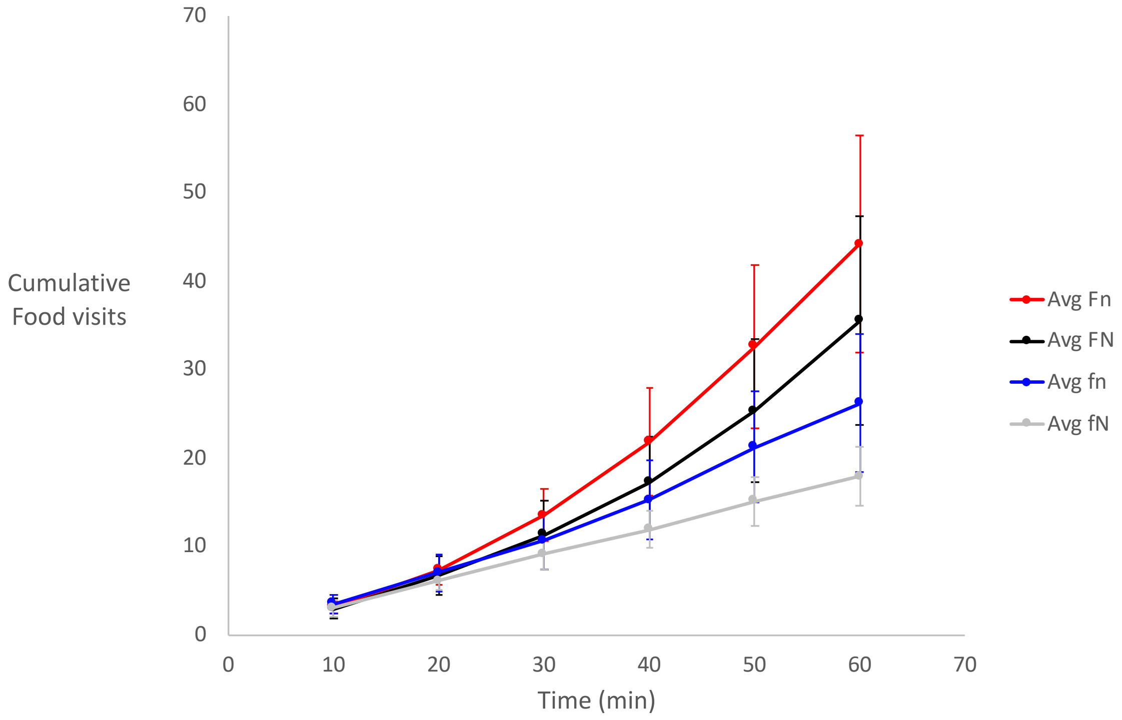


Fig. 3.9. The cumulative number of nest visits, first 60 min after experiment start, ± standard error. In the full ANCOVA model (log transformed) including interactions between model terms, the interaction between food treatment and time was significant (*p* = 0.010) and positive, which means that when ants were less hungry, the cumulative number of nest visits increased faster (higher slopes for LF lines than HF lines). The effect of time was significant ($p < 0.001$) and positive, which means that the cumulative number of nest visits increased with time. Regarding intercepts, the effect of nest treatment was significant ($p < 0.001$) and negative, which means HN > LN. The effect of food treatment was significant ($p < 0.001$) and positive, which means LF > HF.

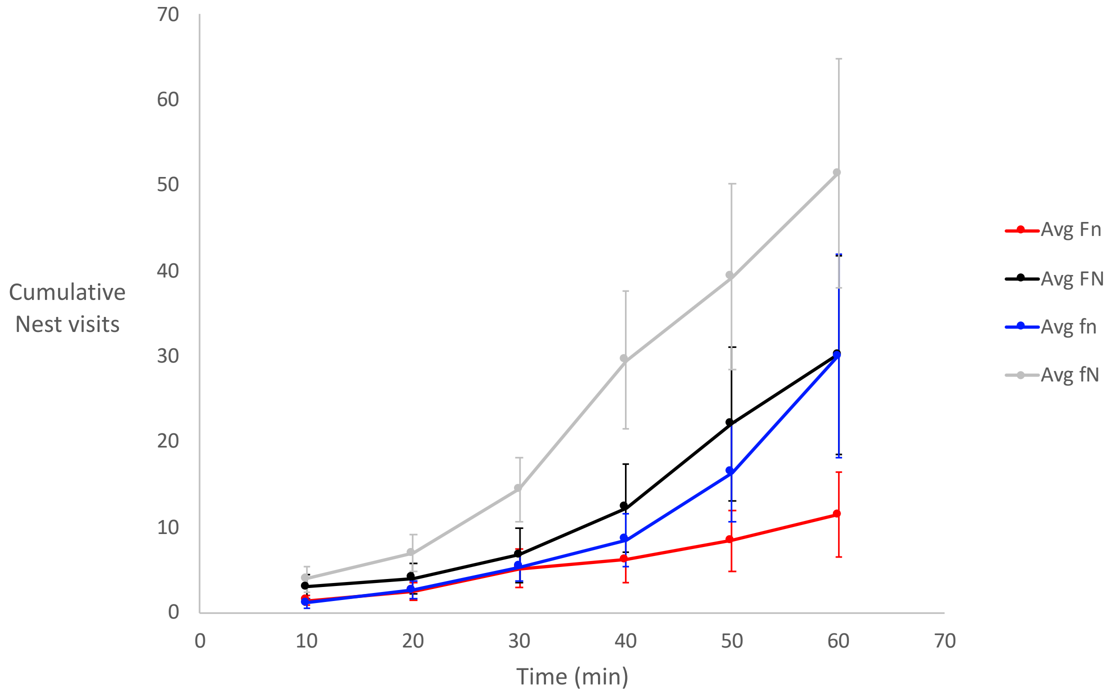


Fig. 3.10. Ants exploring the arena, first 60 min after experiment start, ± standard error. In the full ANCOVA model (log transformed) including interactions between model terms, the effect of time was significant ($p < 0.001$) and negative, which means that the level of exploration decreased with time. The intercepts were positive, so they are meaningful: The effect of nest treatment was significant ($p = 0.015$) and negative, which means that HN colonies started with more exploration than LN colonies. The effect of food treatment was significant ($p = 0.012$) and positive, which means that LF colonies started with more exploration than HF colonies.

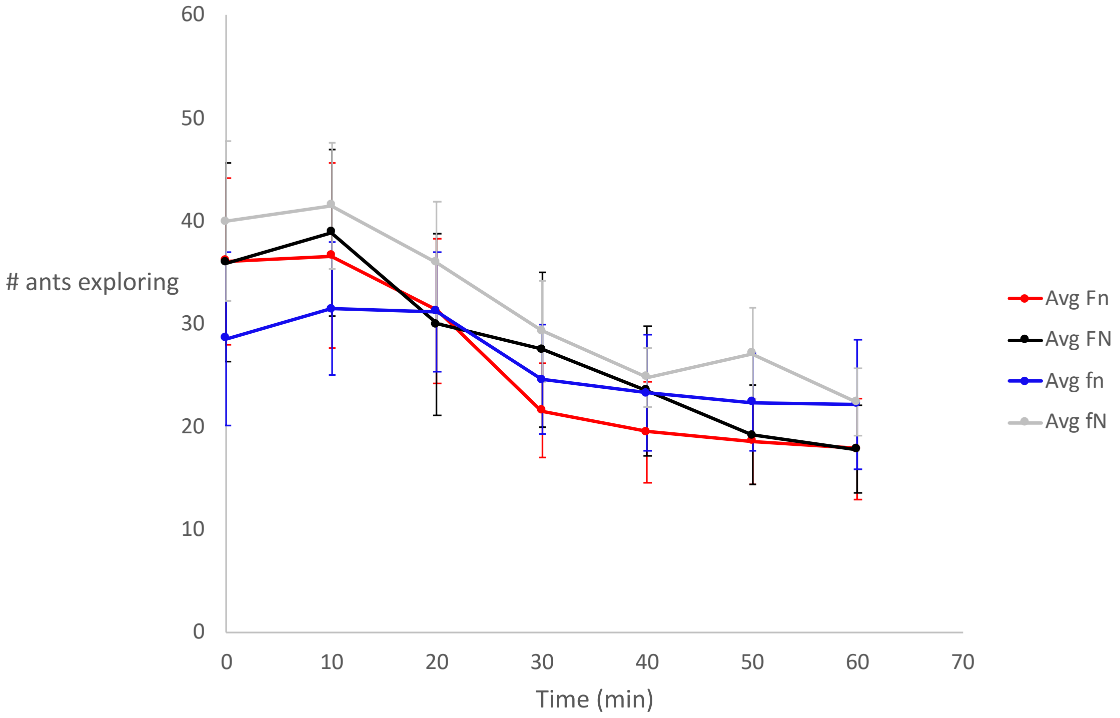


Fig. 3.11. Differential recruitment (= food tandem runs – nest recruitment) for each treatment (first 60 min), ± standard error. *$p < 0.05$ for Kruskal-Wallis test between the four treatments; †$p < 0.05$ for post hoc Nemenyi test between *Fn* and *fN*. Predicted order of food and nest allocation ratio (highest to lowest): *Fn* > *FN* > *fn* > *fN*.

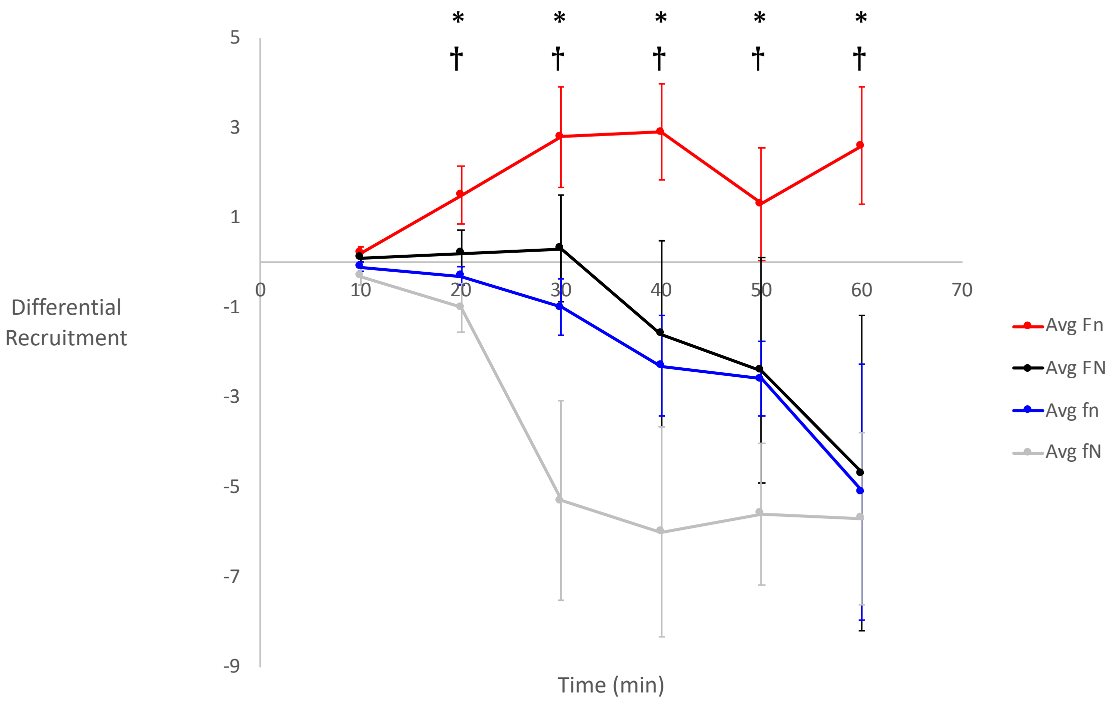
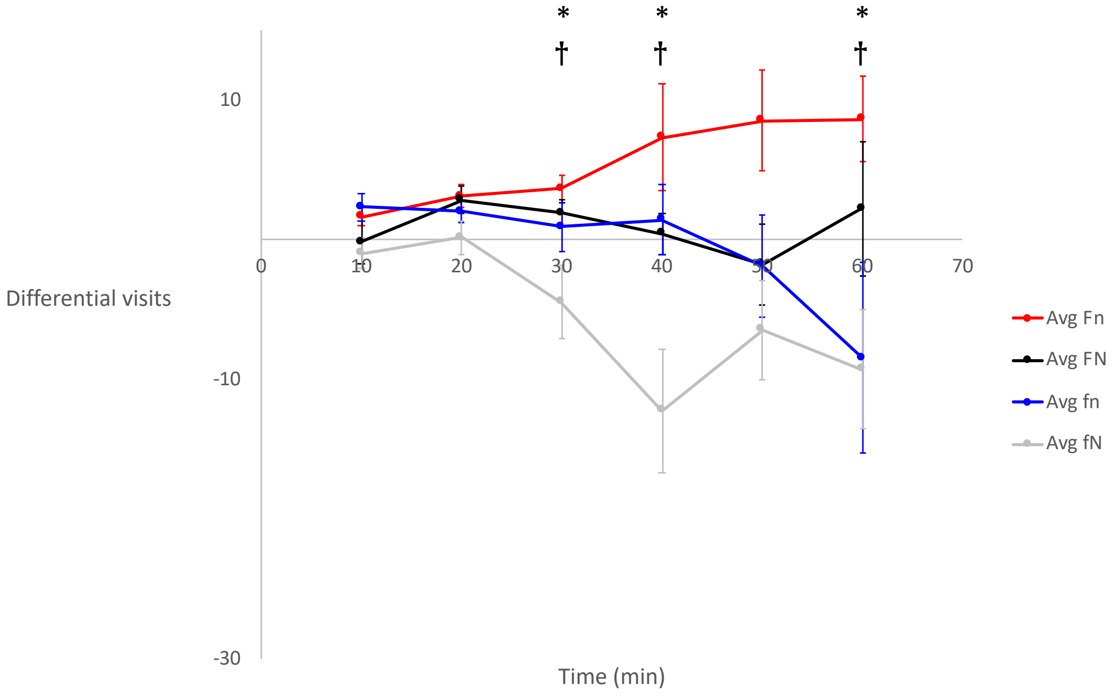


Fig. 3.12. Differential visitation (= food visits - nest visits (change in number of ants rather than current ants in new nest)) for each treatment (first 60 min), ± standard error. *$p < 0.05$ for Kruskal-Wallis test between the four treatments; †$p < 0.05$ for post hoc Nemenyi test between *Fn* and *fN*. Predicted order of food and nest allocation ratio (highest to lowest): *Fn* > *FN* > *fn* > *fN*.



CHAPTER 4

THE TUNED ERROR HYPOTHESIS IN RECRUITMENT AND THE RETURN OF RECRUITS

Abstract

When looking for food or a new home, social insects use recruitment to enlist the help of nestmates by sharing information about the target's location. However, it is not always clear exactly what information the recruits learn. For *Temnothorax rugatulus*, recruiters lead single followers to food and nest target via tandem runs. These recruiters often lose followers before reaching the target, and this prompted me to test the tuned error hypothesis. This hypothesis holds that the directional error in recruitment information is adaptively tuned to the size of the target area. I predicted that error in recruitment information would be larger for food tandem runs compared to nest tandem runs, because food patches generally occupy a larger area than new homes, which are accessed by a small entrance. I found that food tandem runs were more likely to lose followers than nest tandem runs, which supports the tuned error hypothesis and brings the hypothesis into light again. Colonies with food targets started tandem runs earlier than those with nest targets, suggesting that food tandem leaders do not invest as much time learning the visual surrounding as nest tandem leaders.

After recruiters lead followers to the target, followers then navigate subsequent trips to the target alone. Previous studies showed that these ants rely predominantly on visual cues to navigate, but less is known about whether visual learning occurs during tandem following. I hypothesized that the followers learn the visual surroundings while tandem following to visually navigate subsequent trips alone. I tested this by presenting

previous tandem followers with either of two treatments on their subsequent solo trip: a block treatment in which I blocked the visual surroundings with a cardboard cylinder until they reached the target feeder, or a control treatment in which I briefly blocked the visual surroundings with the same cylinder but took it away soon after the ants began their lone trips. The ants with blocked surroundings during subsequent lone trips deviated from their tandem paths at a similar level as control ants, rejecting a role of visual learning during tandem runs. However, control ants were straighter in their lone trips than blocked ants, affirming the role of visual cues in navigation.

Introduction

Recruitment involves bringing a nestmate to a place where work needs to be done, such as foraging, establishing a new home, or fending off an enemy (E. O. Wilson 1971). When the recruiter shares information about a target to assist the recruits in reaching that target, there are two things to consider: first, how precisely should it lead the recruits to the location of the target? Second, at least as important is, once the recruits arrive at the target, how do they find their way back to the target on their own? In this chapter, I investigate both of these questions during recruitment in the ant *Temnothorax rugatulus*.

The first question is relevant in social insects, because recruitment is often imprecise (Deneubourg, Pasteels, and Verhaeghe 1983; Haldane and Spurway 1954). This directional error can be looked as a constraint in performance, or as an adaptive feature of recruitment, as in the tuned error hypothesis (Haldane and Spurway 1954; Towne and Gould 1988). This hypothesis was originally developed for honeybees, and it suggests that directional error in recruitment is adaptively tuned to help spread recruits over an area, allowing them to find novel food patches (Weidenmüller and Seeley 1999). Indeed, foraging error-prone bumble bees are more likely to find novel flowers (Evans and Raine 2014). A previous study found recruitment in a *Temnothorax* species during emigration (Pratt 2008), so in this study, I explored whether this directional error differs between recruitment by *T. rugatulus* during foraging and emigration.

One prediction of this hypothesis is that a target with a wider patch area will elicit greater directional error; recruitment to a food patch will have greater directional error than recruitment to a nest site, a point source defined by a small entrance (Weidenmüller and Seeley 1999). This makes sense from a decision-making perspective as well, in relation to the speed–cohesion tradeoff (Sumpter and Pratt 2009), in which response to food is faster but recruits are split among multiple targets versus a slower response to a nest but all colony members end up together. Greater cohesion to one nest site will result from more precise recruitment. This was supported by results of Weidenmüller and Seeley (1999) in honeybees, because dance angles for the nest site were more precise than dance angles for the feeder. However, Tanner and Visscher (2006) challenged this evidence, because when they controlled for the type of substrate in the two dance contexts (Weidenmüller and Seeley 1999) the two dances had similar directional error in dance angles (Preece and Beekman 2014).

This question is relevant to ants, because recruitment precision is also variable in ants (Deneubourg, Pasteels, and Verhaeghe 1983; E. O. Wilson 1962), and food targets and nest targets likely vary in patchiness too. There is some evidence for the tuned error hypothesis in ants: in *Temnothorax nylanderi*, distance did not have an influence on the recruitment success rate (Glaser and Grüter 2018), which is in line with the tuned error hypothesis in terms of target distance: (Towne and Gould 1988) suggests that honey bees have lower dance error with increasing target distance, such that the distribution of recruits arrival has a constant area with a similar-sized area, regardless of distance.

To test the tuned error hypothesis, I examined food and nest tandem runs in *Temnothorax rugatulus*. The tuned error hypothesis predicts that nest recruiters lead more precise tandem runs than food recruiters. Specifically, I predicted that nest tandem runs will be slower to allow the follower to learn the route better: slow tandem runs might be better for learning because Franklin et al. (2011)'s fully sighted tandem pairs have slower tandem runs than visually impaired tandem pairs. Another variable that might be indicative of precision is the loss rate: often *Temnothorax* tandem leaders lose their followers (Möglich 1978; Shaffer, Sasaki, and Pratt 2013), about 70% for *T. curvispinosus* (Pratt 2005; 2008). These tandem runs are still useful for followers, because 21% of lost followers in *T. albipennis* (Franks et al. 2010), and 40% of lost followers in *Camponotus consobrinus* (Schultheiss, Raderschall, and Narendra 2015) reached the target after a period of searching. I predict that nest tandem runs will also have a lower loss rate for followers. A higher loss rate in foraging tandem runs will result in end locations of tandem runs that are more spread out than those in emigration. Therefore, I compared the loss rate between foraging and emigration tandem runs to test the tuned error hypothesis.

The second question is, once the recruits arrive at the target, how would they return to that target on their own? Because recruitment is a form of communication, a recruiter does not simply take a nestmate to the location, but often shares information about the target such as how to get there. In social insects, this navigational information can be transmitted directly as in honeybees via the dance language (Dyer 2002) or implicitly by providing a guide, such as a pheromone trail or the recruiter itself. In implicit navigation, the recruits who follow the guide learn an aspect of the route that helps them return to the target, by learning the visual surroundings.

In trail-laying ants, some evidence suggests that the pheromone trail affects how followers learn the visual surroundings (Hölldobler 1976; Klotz 1987; Harrison et al. 1989; Aron et al. 1993; Grüter, Czaczkes, and Ratnieks 2011; Grüter et al. 2015; Czaczkes et al. 2011; 2013). In this case, the trail can serve as a guide even on subsequent lone trips, so recruits that have not learned the visual surroundings can still easily reach the target. It is different in a tandem run, wherein the recruiter serves as a guide: An ant that has found a resource returns home and leads one or several ants to the target. When the tandem run ends, the follower needs to navigate subsequent trips alone (Hölldobler, Möglich, and Maschwitz 1974; Möglich 1978; Pratt et al. 2002), so it is more critical for the follower to learn visual or other navigational cues during the tandem run than in trail-following ants.

In this study, I also examine the hypothesis that *Temnothorax* tandem followers learn visual cues during following. It is often assumed that they do this (Franks and Richardson 2006), but direct evidence is lacking. There is some indirect evidence or indication that make the hypothesis plausible: *Temnothorax* ants use visual cues to navigate (Aron, Deneubourg, and Pasteels 1988; Pratt, Brooks, and Franks 2001; McLeman, Pratt, and Franks 2002; Bowens, Glatt, and Pratt 2013), and have relatively high optical sensitivity (Ramirez-Esquivel et al. 2017). This suggests that they learn surrounding visual landmarks like other ants (Collett, Chittka, and Collett 2013). The speed of a tandem pair during pauses was affected by the presence of conspicuous landmarks (Franks and Richardson 2006), and Basari, Bruendl, et al. (2014) found support for learning during tandem running by displacing landmarks for former followers. However, ants visually impaired with paints could still follow and lead tandem runs, although their paths were less smooth and faster than unimpaired tandem runs (Franklin et al. 2011). Also, Franklin and Franks (2012) showed that the tandem path and the follower's own later tandem path were not similar. Because of the indirect evidence and ambiguity of learning during following, I tested the following competing hypotheses:

1. Tandem followers visually learn the surroundings during tandem running.

2. Tandem followers are not learning; they are simply following the leader.

If tandem followers visually learn the surroundings while following, I predicted that when the visual surroundings are obstructed during the followers' subsequent independent trips, their visual navigation will be affected (because the visual surrounded that they learned will not be visible) and they will have less straight paths to the target compared to followers whose view is mostly unobstructed. More importantly, the independent path will deviate more from the tandem path, because the obstruction will prevent the followers from using the learned information to recapitulate the tandem path on their independent paths. If the tandem followers are simply following the leader and not learning, I predicted the followers with obstructed views and unobstructed views will have similar paths to the target, and there will be no difference in the deviation of the independent path from the tandem path between the two view treatments.

Methods

Subjects

I collected *T. rugatulus* colonies from the Pinal Mountains in Arizona (N 33° 19.04' W 110° 52.38') in September 2017. All colonies had one queen, 40–220 workers and brood. Following collection, colonies were housed on laboratory benches, then about two weeks before I started Experiment 1, I moved them to a diurnal incubator. The incubator was kept at a 14:10 L:D schedule at approximately 22 °C and 15 °C (light and dark periods, respectively). I maintained colonies as described in Sasaki et al. (2015), feeding them an agar-based diet (Bhatkar and Whitcomb 1970) and housing them in nests made of a 2.4 mm-thick balsa slat sandwiched between two glass microscope slides (50 X 75 mm).

Experiment 1: Are tandem recruitment to food and nest different?

To test whether food and nest tandem runs show differences in their paths, I induced food tandem runs and nest tandem runs in separate experiments. I ran these experiments in November – December 2017. For both foraging and emigration experiments, I placed the home nest and the target 30 cm from home nest entrance in a 50 X 50 cm arena. I soon started the experimental trial between 12:30 pm and 6 pm. Each trial lasted between one hour to three hours and a half. I recorded each trial with a SONY FDR-AX53 camera, recording at 4K resolution.

For foraging trials, I deprived the colonies of food for 14-15 days (these ants are highly resistant to food deprivation; Rueppell and Kirkman (2005). The food target was 0.1 ml of 0.25 M sucrose solution in a glass depression slide. I used seven colonies, and observed a total of 12 complete tandem runs (i.e., tandem runs that reached the target with the pair still in contact). Five colonies yielded two complete tandem runs while two had one complete tandem run each. Once or twice per trial, I noticed that the sucrose solution was thickening due to drinking or evaporation, so I replenished the feeder with 0.05 ml of the same solution.

For each emigration trial, I placed a colony in the arena and then I removed the roof. The nest target was the same high-quality nest design described in the second and third chapters (Fig. 4.1; Inkscape Project 2017): a rectangular 40 X 65 mm balsa cavity in between two microscope slides, with light filters on top for a dark interior. I observed seven colonies; six colonies yielded two tandem runs each for 12 complete tandem runs.

For both foraging and emigration experiments, I used only colonies that were not used for any experiment previously and used each colony once, to minimize the effect of prior learning on the properties of tandem runs in my experiment. One exception, a colony in emigration experiment, was used in a different experiment about 40 days before. I do not expect this exception to be an issue, because Langridge, Franks, and Sendova-Franks (2004) shows that when inter-trial interval between two emigration trials is longer than 6 days, second emigration is not significantly faster than the first. I attempted to match colony sizes between colonies used for foraging and emigration experiments. Within each experiment, I aspirated the tandem leader if it got close to reaching the target (whether with or without follower), to avoid measuring the same leader twice.

Tandem follower loss rate

To measure recruitment success for food and nest tandem runs, I used loss rate, which is the proportion of tandem leaders reaching the target without a follower. For each trial, I looked at up to first four tandem runs with the leader reaching the target at the end (or in most cases, I aspirated the leaders just before they reached the target to avoid recording the same tandem leader twice). A tandem run was considered complete if the tandem leader arrived at the target with a follower or reached the target in or less than 10 sec after losing the follower. If a tandem leader reached the target alone and lost its follower before that 10 sec window, the tandem run was counted as lost. Of the seven colonies I used for nest, one colony did not yield a complete tandem run that I could track, but it did yield three tandem runs for comparing loss rates. Because a previous study found that 20% of lost followers still reach the target (Franks et al. 2010), I predict that loss rate would be higher for food than nest tandem runs per the tuned error hypothesis: it would be beneficial for the recruit arrivals to be more spread out, and a greater loss rate would result in more followers that end up in a location away from the target. I organized the data into a contingency table (Table 4.1) and used Fisher's exact test to compare the loss rate between food and nest tandem runs. For foraging, there were three lost tandem runs that I did not include: I failed to aspirate these tandem leaders, so I did not include these to avoid possible pseudoreplication with later tandem leaders. I could not aspirate and did not count two more lost leaders, one in foraging and one in emigration, because they got superimposed with other ants and I could not follow them to the target. It is possible that I counted later tandem runs by these five ants, which would have more experience reaching the target than other ants.

Latency to a tandem run

To measure whether recruitment starts faster in foraging or emigration, I measured the time of first tandem run (lost or complete) for each trial. I subtracted the respective target discovery time from each time of first tandem run to account for a possible difference in discovery time between foraging and emigration. To test whether the time is earlier for foraging or emigration, I used R package 'survival' for survival analysis with Cox proportional hazard model (Andersen and Gill 1982; Therneau 2015; Therneau and Grambsch 2000). Glaser and Grüter (2018) reported that tandem success rate increases with leader experience in another *Temnothorax* species, so I predict that the first tandem run will start sooner in foraging, with lower leader experience: in line with my prediction above that loss rate for food will be higher, and this could be a mechanism behind the predicted difference in loss rate.

To measure whether a complete recruitment happens faster in foraging or emigration, I measured the time of first complete tandem run for each trial. I used the same analysis method as first tandem run (lost or complete) above. Given that both food and nest tandem runs here are those reaching targets with followers, which would be more likely with more leader experience, I predict that this time will be similar between foraging and emigration.

Straightness, duration, and directional change

To measure how directly the tandem leaders reach the target, I traced the trajectory of the tandem leader for each path: I used Adobe Premiere to convert the video into image sequences, then used Fiji (Schindelin et al. 2012) to manually track the location of the head of the leader. This resulted in a file with a list of XY coordinates. For each path, I measured straightness using R package 'trajr' (McLean and Volponi 2018). Straightness is D/L, where D is the beeline distance between the first and last points of the path, and L is the path length between the two points (Batschelet 1981). I used straightness, a reliable estimate of the orientation efficiency, rather than sinuosity (Benhamou 2004). Benhamou (2004) raises three limitations of the straightness index, but these are addressed in this experiment, because the ants did not have any obstacles in the arena, they did not show patterns of edge following, and I fixed the step length with five tracking points per second (Benhamou 2004), which gives a high recording frequency given that even relatively fast transporters in another *Temnothorax* species run 4.6 mm/sec (Pratt et al. 2002). In a similar vein, I measured the duration of the tandem paths, from leaving home nest to reaching the target, to see how long it takes each ant to reach the target. Per the tuned error hypothesis, I predict that food targets would have tandem runs with less straightness and longer duration, because food targets are expected to be more patchy than nest targets, and result in tandem paths that spread out the end locations of tandem runs more than nest tandem paths.

I also measured the directional change (in degrees) of the path for each step length, then calculated mean directional change and standard deviation of directional change, using R package ‘trajr.’ I expected mean directional change to give a measure similar to straightness, but thought that standard deviation would give a measure of how variable the paths are in directional changes. Per the tuned error hypothesis, I predict that food tandem runs will have a higher standard deviation of directional change, because a tandem path with a higher variance in directional change is expected to have a greater spread in the end locations of tandem runs.

Recruitment probability of targets

To measure the respective quality of food and nest targets, I did as follows. I calculated the probability of recruitment by allowing the ants to have a fixed number of visits, then measuring the number of recruitment events (described in detail in Chapter 2). The value for the nest design used in emigration experiment above (Fig. 4.1) was measured as 0.24 in Chapter 2. For 0.25 M sucrose solution used for the foraging experiment here, I measured the recruitment probability in March 2018. I used seven colonies, with colony size ranging from 70 to 220 workers.

In the evening, I placed the home nest in a ~22 x 22 cm plastic arena, and put the lid on overnight. Next day, I lifted the lid, then placed the feeder glass slide 10 cm from the home nest entrance and waited at least 10 min before presenting 0.25 ml of 0.25 M sucrose solution on the feeder. I then counted the number of visits by ants to the feeder and the number of tandem recruitment events until the 20th visit. After the 20th visit, I aspirated any ant approaching the feeder, taking care not to disturb the drinking ants. After the last drinker left the feeder, I removed the feeder to prevent more visits. I then waited for more tandem recruitment for at least 10 min after removing the feeder. I waited for the activity (presumably stirred by recruitment attempts by visitors) in the home nest to settle down. I then counted the number of tandem recruitment events in each trial and divided that number by 20, the number of visits. The average value for recruitment probability based on this estimate was 0.435 ($N = 7$ colonies; 61 tandem runs, of 140 total visits).

Experiment 2: Do tandem followers learn visual surroundings?

To study follower learning during a tandem run, I motivated the ants to forage by depriving them of food for 14 days. I ran these experiments in November 2017. In each trial, a hungry colony in its nest was placed in a 50 x 50 cm arena with corners restricted by wooden enclosures (Fig. 4.2) to facilitate blocking the visual surroundings later. I soon started the experimental trial, between 12 pm and 7:30 pm, by presenting the ants with 0.1 ml of sucrose solution in a feeder about 30 cm away from the nest entrance. The feeder consisted of a glass depression slide and contained good-quality food (1.0 M sucrose). Whenever an ant reached the feeder to drink, I marked these visitors with an orange paint mark (Testor's Pactra car lacquer paint) to aid in keeping track of them. When a tandem run started and reached the feeder, with the follower drinking at the feeder, I marked this drinking follower with a green paint mark. I followed these green followers back home, and when one of them was about to exit the home nest alone to return to the feeder, I gave it one of two treatments:

1. Block treatment: Block the visual surrounding with a cardboard cylinder, 50 cm in diameter and 20 cm in height, until the green ant reached the feeder.

2. Control treatment: Block the surrounding with the cylinder, then immediately lift the block. I did this to control for the effect of a large object looming over the ants, but because I had the cylinder for a short amount of time, the green ant could see the visual surrounding for most of its path to the target.

I attempted to run one block treatment and one control treatment per colony in the same trial, pseudorandomizing the first treatment for each colony. Each colony was used only once to prevent visual learning across trials from affecting the results. Nine trials had one of each treatment, and two trials had only one control each, yielding nine block replicates and 11 control replicates. Each trial lasted between one hour and a half to four hours. I recorded each trial with a SONY FDR-AX53 camera, recording at 4K resolution to track the ants. Once or twice per trial, I noticed that the sucrose solution was thickening due to drinking or evaporation, so I replenished the feeder with 0.05 ml of the same solution.

Difference between tandem and follower's independent path

To test whether the green followers showed evidence of learning during tandem following to the feeder, I measured how much the follower's independent path deviates from the tandem path it was led on. I measured this deviation by taking the difference between the two paths. I predicted that if followers learn the visual surrounding during tandem following, the difference would be greater for block trials than control trials. This is because in block trials, the surrounding that followers have visually learned will largely be invisible to the followers, leading to a greater deviation from their learned path. In control trials, the surrounding that the followers learned will mostly be visible, so followers should use what they learned to imitate the tandem paths. I also ran Levene's test between the difference in block trials and the difference in control trials, to see if variances are unequal between the two groups.

I calculated the difference between tandem and independent paths as follows. For each path, I traced the path to create a trajectory (Fig. 4.3). I used similar programs as in experiment 1 above: I used Adobe Premiere to convert the video into image sequences, then used Fiji to manually track the location of the head of the follower in each path. This resulted in a file with a list of XY coordinates for each path. To calculate the difference, I used scripts in Perl (Christiansen et al. 2012) and R package 'BSDA' (Arnholt and Evans 2017) to get an average-x value for each y value, to create an average-x path. This ensured that there is only one x value for any given y value for the tandem path. I created an average-x path for the independent path as well. Using the same scripts, I took the difference between average-x of tandem path and average-x of independent path, for each y value.

Straightness and duration

To measure how directly the followers reach the target on their independent trips, I measured the straightness of each independent path, as in experiment 1 above. I predict that the independent paths of the block trials would be less straight than those in control trials. This is because I expect the ants in block trials would have less of the visual surrounding visible to them. This would lead to them having more difficulty finding the target than those in control trials, leading to a more wandering path. In a similar vein, I measured the duration of each independent trip, from leaving home nest to reaching the feeder and drinking, to see how long it takes each ant to reach the target. I predict that the independent paths of block trials would take longer than those in control trials, because I expect those in block trials would have more difficulty finding the target, as explained above.

Other statistical analyses

I used R software (v. 3.5.1) for all these tests (R Core Team 2018). Because I collected continuous data for these variables, I used the Mann-Whitney-Wilcoxon test (Hollander and Wolfe 1999), or two-sample *t*-tests based on the following criteria: If the distribution was not normal, based on the normal QQ plot and the Shapiro-Wilk test but the samples had homogeneity of variances in Levene's test (Fox and Weisberg 2011), I used Mann-Whitney-Wilcoxon test. If a distribution was normal based on the normal QQ plot and Shapiro-Wilk test but variances were heterogeneous based on Levene's test, I used a two-sample *t*-test assuming unequal variances (Welch two-sample *t*-test). If a distribution was normal but variances were homogeneous, I used a two-sample *t*-test assuming equal variances.

Results

Food versus nest

Food tandem paths had a significantly higher loss rate than nest tandem paths (Table 4.1; Fisher's exact test: $p = 0.048$), which matches the prediction of the tuned error hypothesis.

The first tandem run (whether lost or completed) for each colony started significantly sooner for food than for nest, even after adjusting for target discovery time

(Fig. 4.4; Cox proportional hazard model: $p = 0.032$; food discovery times were significantly faster than nest discovery (Fig. 4.5)). This matches my prediction under the tuned error hypothesis: food tandem leaders gain less experience for a greater loss rate, and this results in colonies with food targets starting tandem runs earlier. This also makes sense given that my food target has a greater recruitment probability than my nest target. When I only counted complete tandem runs for the time of first tandem run, there was no significant difference between food and nest tandem runs (Fig. 4.6; Cox proportional hazard model: $p = 0.32$), which matches my prediction under the tuned error hypothesis.

Among complete tandem paths that I analyzed, food tandem paths were straighter (Fig. 4.7) and reached the target faster than nest tandem runs (Fig. 4.8), although the differences were not statistically significant (two-sample *t*-test for straightness: $p = 0.14$; Mann-Whitney for duration: $p = 0.11$). These results did not match my prediction that food tandem runs will be straighter and reach the target later than nest tandem runs, and did not support the tuned error hypothesis.

Mean directional change was statistically similar between the two treatments (two-sample *t*-test: $t = 0.81$, $df = 22$, $p = 0.43$; mean values: 126.3° for food, 121.8° for nest) as well as the standard deviation of directional change between the two treatments (two-sample *t*-test: $p = 0.77$; mean values: 118.7° for food, 117.5° for nest). These results do not match my prediction under the tuned error hypothesis.

One thing to consider for food versus nest: it is probably easier for the tandem pair to reach the sugar water part of the feeder than enter the 1-mm-wide entrance for the new nest. This could be the reason why discovery time for food is faster than nest (Fig. 4.5). Also, in food, the tandem paths start from a single entrance from home nest, but in nest, the tandem paths start from any side of home nest, because the roof is removed to encourage emigration. This could lead to a greater variation in the path for nest.

Block experiment

The difference between tandem paths and independent paths was statistically indistinguishable between block and control treatments (Fig. 4.9; Welch two-sample *t*-test: $p = 0.78$). This does not match my prediction with learning during tandem following, although the difference for controls was slightly lower (mean for block = 225.1, mean for control = 215.3). The difference for controls had a significantly higher variation (Levene's test: $p = 0.008$), which might mean that the followers do learn during tandem following, but this learning ability varies between individuals.

The independent paths for control treatments were significantly straighter (Fig. 4.10; two-sample *t*-test: $p = 0.010$), which matches my prediction with learning during tandem following. These paths also reached the target sooner for control treatments, although the difference was not significant (Fig. 4.11; Mann-Whitney: $p = 0.057$). A significant difference in path duration between the two treatments would have matched my prediction, but the difference was not significant.

Discussion

Food and nest experiments to assess differences in tandem runs

Food tandem runs had a significantly greater loss rate than nest tandem runs (Table 4.1). This supports the tuned error hypothesis (Preece and Beekman 2014), in that the food source, which likely has a larger patch area than a nest target with a small entrance (*Temnothorax* ants prefer nests with small entrances, Pratt and Pierce 2001;

Sasaki and Pratt 2013), had a greater loss rate. The point where the follower loses contact with the leader and starts searching independently is predicted to be more spread out for food tandem runs to explore and exploit a larger area, resulting in more food sources for the colony. Indeed, it is reported that these ants forage for small arthropods such as Collembola and insect larvae as well as scavenging crickets, spiders, and beetles (Bengston and Dornhaus 2015), which are food items that are likely patchily distributed. Wheeler (1910) reported *Leptothorax* foraging on honeydew drops from hemipterans (Shaffer 2014), which might be more concentrated, but there could be several aggregations of hemipterans in a given area. On the other hand, in nest tandem runs where complete tandem runs are more common, more followers reach the target with the leader, so the follower does only minimal searching around the target. This same pattern in the difference in loss rate could also arise due to selection pressure to have a higher recruitment accuracy for nest recruitment (Preece and Beekman 2014). It would be difficult to empirically distinguish whether the difference in error rate between food and nest recruitment arose because it is beneficial to have a higher error rate for food, or because it is beneficial to have a lower error rate for nest.

The difference in loss rate could arise due to differential need for consensus, instead of target area: Perhaps nest recruitment has a lower loss rate because once a target is found, many ants must visit the target as the colony moves (and gain benefit from the find), whereas for food, even a couple ants that find a food source can exploit it and bring it back to the nest, putting the target to use.

The difference in loss rate is not simply the result of differences in recruitment probability, because the food target (0.25 M) with a greater loss rate had a higher recruitment probability than the nest target. If recruitment probability determines loss rate, then I expect that the targets with higher recruitment probability would have a lower loss rate, because the target is more desirable than one with lower recruitment probability. Individual differences might affect the loss rate: Perhaps some follower ants are more prone to get lost than others, some leaders are not as good at leading a tandem run, or a combination of the two. In bumblebees, some individuals are more error prone than others (Evans and Raine 2014).

The mechanism of the difference in loss rate could be due to different tandem run properties between food and nest targets. It is possible that food tandem leaders are more likely to give up leading the follower than nest tandem leaders. Among complete tandem runs, those in foraging were faster to target and were straighter than those in emigration, although the differences were not significant. The differences (if food tandem leaders walk faster than nest tandem leaders) could lead to the followers having a more difficult time following food tandem runs all the way to the target. Food tandem runs might have had a greater standard deviation of directional change as predicted under tuned error hypothesis, but mean directional change and the standard deviation of directional change were both statistically indistinguishable between food and nest tandem runs. Another explanation for the difference in loss rate is that it arises from different task groups. In the ant *Lasius niger*, scouts are less likely to respond to trail pheromones and more likely to leave a trail pheromone than recruits (Detrain, Pereira, and Fourcassié 2019). Perhaps scouts are more likely to explore and find more food than recruits (Deneubourg, Pasteels, and Verhaeghe 1983). Other examples of similar behavioral variation include producer versus scrounger (Stephens and Dunlap 2017) and slow explorers that utilize previous information (personal or social) versus fast explorers that explore more randomly (Smit and van Oers 2019) in birds. It could be that in *T. rugatulus*, loss rate could vary depending on properties of target such as food abundance. Mottley and Giraldeau (2000) found that in spice finches, as frequency of scroungers increased, benefit of being a scrounger went down.

Given the difference in loss rate of tandem runs in *T. rugatulus*, it would be interesting to see if a similar pattern is found in the honeybee waggle dance. Previous research identified differences in the precision of the dance angle between food and nest dances (Weidenmüller and Seeley 1999; Beekman et al. 2015), but perhaps the arrival rate of recruits should be looked at instead. One could control the substrates to keep the dance angle precision similar between food and nest dances (Tanner and Visscher 2006), then measure whether the arrival rates of recruits differ by context (while controlling for the effect of the Nasanov gland for emigration; Seeley 2010). One difference between recruitment in honeybees and *T. rugatulus* is that in honeybees, if the waggle dance is imprecise, then there is less chance that the recruit will reach the target. In *T. rugatulus*, whether the tandem path is straight or not, if the tandem pair reaches the target, the follower reaches the target (although a less straight path could have a higher loss rate). Instead, a less straight path is expected to have a bigger impact on the follower's independent path, which might make the follower's return to the target more challenging than if the tandem path was straighter.

In honeybees, dancers are more likely to dance with constant number of waggle runs (a proxy for quality; Seeley 2003; Seeley, Mikheyev, and Pagano 2000) across trips for food as opposed to dances in nest, which decrease the number of waggle runs across trips (Visscher 2007). It will be interesting to see if *T. rugatulus* or other ants with recruitment systems show a difference in persistence by context. Recruiters for the better feeder gave up followers less than those for the poor feeder (Shaffer 2014), and recruiters for the better nest gave up followers later than the poor nests (Richardson et al. 2007).

First tandem runs (whether complete or lost tandem runs) started significantly faster for food than nest targets (Fig. 4.4). Perhaps food tandem runs start sooner than nest tandem runs, because food tandem runs do not need to be as accurate (Table 4.1), and so leaders spend less time learning the route to the target before starting a tandem run (tandem leaders with more experience have a higher success rate; Glaser and Grüter 2018). On the other hand, ants could start tandem runs for food faster because they regard food as more important than a nest. Or it could be that the combination of food needs and the target food's quality motivates them to recruit faster than the combination of nest needs and the target nest's quality. The time of first recruitment is expected to differ based on the target property, because the latency to recruit for a nest visitor depends on nest quality: Visitors to better nests start tandem runs sooner (Mallon, Pratt, and Franks 2001). There are other possibilities: Food visitors could be more energetic because of recent sugar intake from the visit and start recruiting sooner than their nest counterparts simply because they move faster. It is also possible that when visitors return to the home nest to recruit, more ants are available to recruit for food targets because the home nest is not destroyed. Therefore, most ants stay in the nest as opposed to a nest tandem run, wherein the home nest is missing a roof and ants originally in the nest often scatter around the arena. The tandem leaders attract followers via a tandem pheromone (Möglich

1979; Möglich, Maschwitz, and Hölldobler 1974), which would be easier inside a closed nest when foraging rather than in open space during emigration.

The difference between food and nest tasks regarding the time for the first tandem run might be largely due to the difference in loss rate between food and nest tandem runs. When I eliminated the tandem leaders that lost followers and only counted complete tandem runs when comparing the time of first tandem runs, there was no significant difference between food and nest tasks (Fig. 4.6).

Regarding the difference in time to start a tandem run, how do I know if ants regard food as more important than a nest? There are two ways in which this could be played out. First, place ant colonies in a situation such that given the level of food needs and the quality of the food target, the recruitment probability for a colony in food need A with food quality A is the same as the recruitment probability for the same colony in nest need B with nest quality B. Then present both food A and nest B to the colony, control for the discovery rate, and see to which target the colony expends more recruitment effort. Second, the scale for recruitment probability could be different between food and nest tasks. For example, for food, the recruitment probability could range from 0 to 1, whereas for a nest, recruitment probability might have an upper limit. No matter how dire or good the nest condition, the recruitment probability for nest tasks ranges from 0 to 0.7. It is also possible that the new nest that I offered in this study was not good enough in quality for the ants; there might be ways to make the nest even better or the original nest condition more dire so that its recruitment probability matches that of the food targets.

It is also possible that the first tandem run happened faster in food, because there were more ants ready to lead tandem runs in food compared to those in nest. If there were more tandem leaders, this means that there is a higher chance of leading a tandem run, and this also means that tandem runs would happen earlier, by chance.

The tuned error hypothesis posits that the error rate of recruitment to a target is adaptively related to that target's spatial distribution (Preece and Beekman 2014). The error rate could also be determined by other factors: (a) urgency of the need for the target, because *T. rugatulus* ants are highly resistant to starvation (Rueppell and Kirkman 2005), so the colony can survive a long time without additional food but might need a new nest immediately if its original home is destroyed through a more precise recruitment; (b) constancy of the target, given food could be more ephemeral (more competitors or difficulty locating moving food), whereas nests are usually more stable (crevices in granite rocks): a more stable resource having a more precise recruitment; and (c) additional cues that might differ between food and a nest. For food, odor cues might be associated with the target that aids in finding the target, whereas a nest recruit might rely more on the visual surroundings. In honeybees, dancers for food bring a floral odor that the recruits use to pinpoint the source (Dyer 2002), but dancers for a nest return to the swarm with dirt (Seeley 2010) that probably provides little odor guidance to the target nest.

Block experiments to investigate follower learning during tandem runs

In block experiments, I did not find evidence of learning the visual surroundings while following on a tandem run: The difference between tandem paths and subsequent trips by followers (independent paths) was not statistically distinguishable between the block and control treatments (Fig. 4.9; Franklin and Franks 2012). This lack of difference could be because on subsequent independent trips, followers rely on a chemical orientation trail (Aron, Deneubourg, and Pasteels 1988; Basari, Laird-Hopkins, et al. 2014). On the other hand, the variance of the difference (between tandem and independent paths) for controls was significantly larger than that of block treatment, which could be because followers do learn, but vary in their ability to emulate the tandem path during their independent trip (trail-following accuracy in *Lasius niger* varies by task groups; Detrain, Pereira, and Fourcassié 2019).

The control independent paths were significantly straighter and reached the target faster (although not significantly) than block independent paths (Fig. 4.10 and Fig. 4.11), which suggests that the block interfered with follower navigation on the independent paths. This is consistent with the finding that visual surroundings affect navigation for *T. rugatulus* (Bowens, Glatt, and Pratt 2013; Basari, Bruendl, et al. 2014), and not consistent with the idea that the followers rely on a chemical orientation trail.

Conclusion

I found that food tandem runs had a higher loss rate than nest tandem runs, which supports the tuned error hypothesis and suggests that tandem runs are sensitive to target properties such as the patch area of the target. Colonies with food targets also started tandem runs earlier than those with nest targets, which suggests that colonies respond more quickly to food and may reveal the relative importance of food versus nests to these colonies. These results suggest that other recruitment systems could have a similar difference between food and nest tasks or between other contexts, opening an interesting comparison of recruitments by the same social system in different contexts.

I did not find support for visual learning during tandem following, although I did see higher variation in the difference between tandem and independent paths for controls as opposed to the block treatment, which could be a result of variation in learning by followers. I also found evidence that blocking interfered with follower navigation: Independent follower paths for controls were straighter than those of blocks.

Fig. 4.1. 3D representation of the new nest design: entrance area = ~ 1.5 mm^2, cavity volume* = ~ 5.2 ml, light level in the nest = 4.99 lux. This figure was also used in Chapter 2.

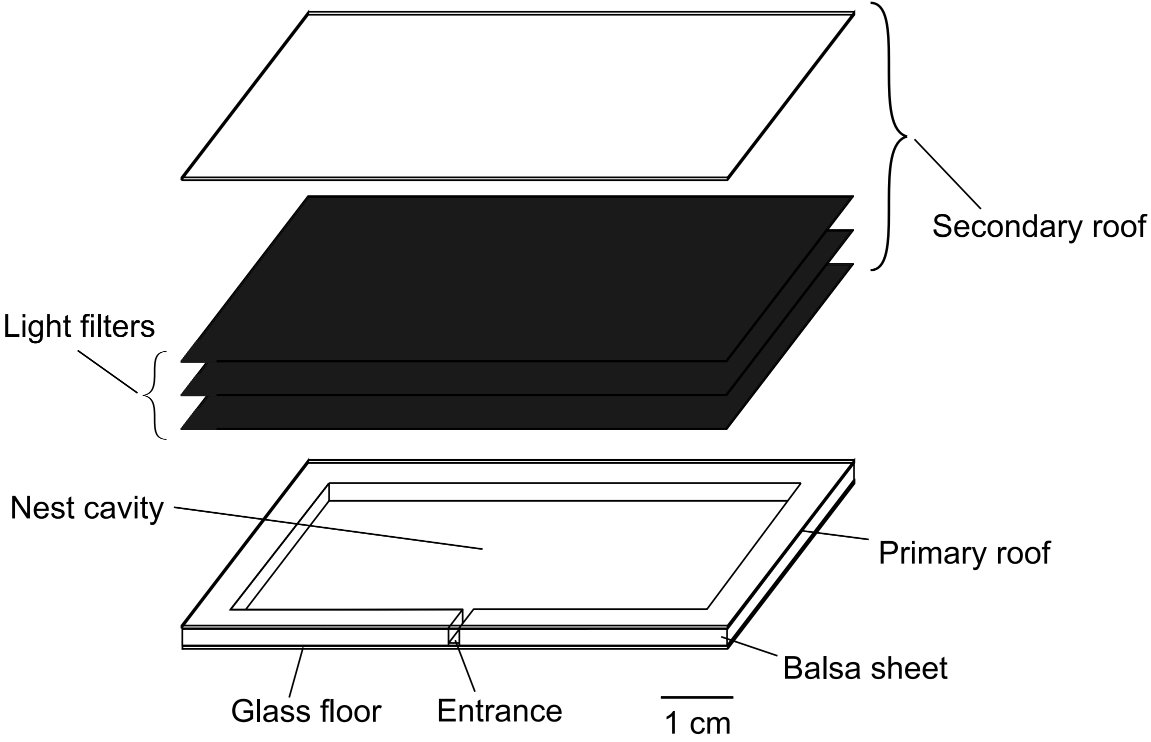


Fig. 4.2. A schematic representation of the experimental arena for block experiments.

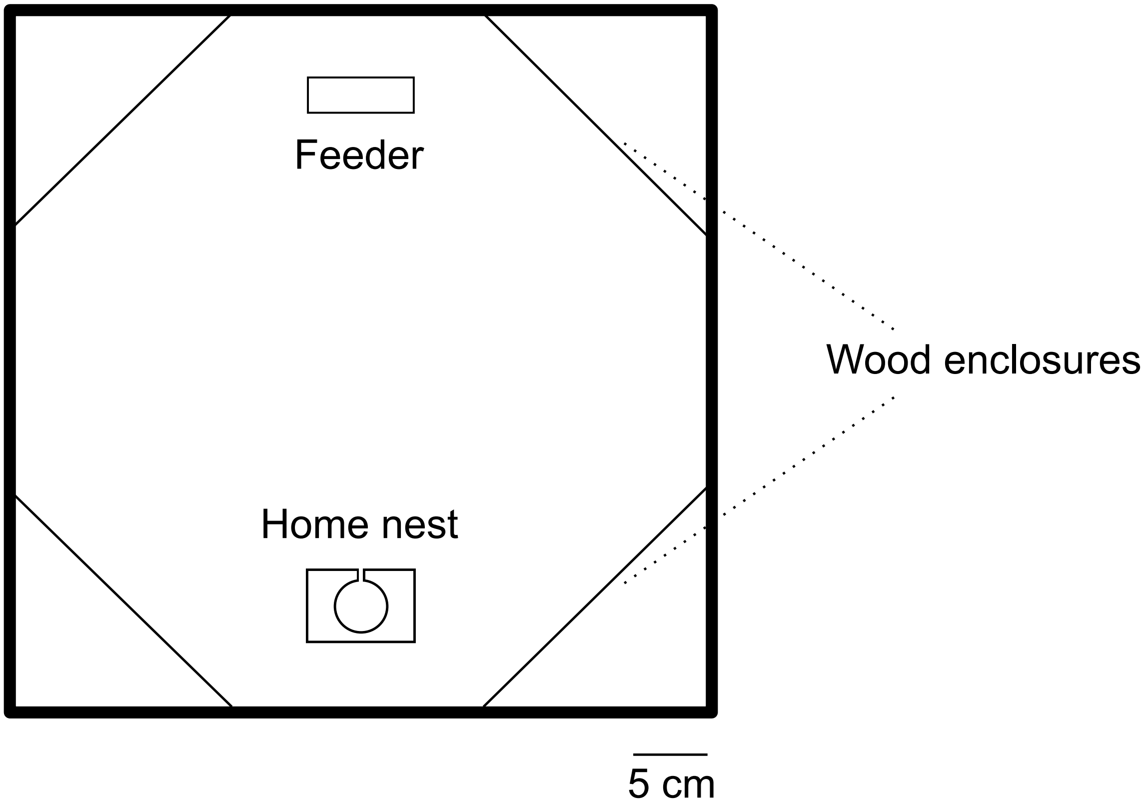


Fig. 4.3. One follower ant's tandem path and its subsequent independent path, to illustrate how I calculated the difference between the two paths. For example, in the independent path, for y = 1500, there are at least three x values, so these x values are averaged to give a single x value for y = 1500. This is applied to the whole path, so that each y value has only one x value. Both paths start at home nest entrance, which is at the top around y = 1500. A point is taken every 5 frames (each video consists of 29.97 frames per second).

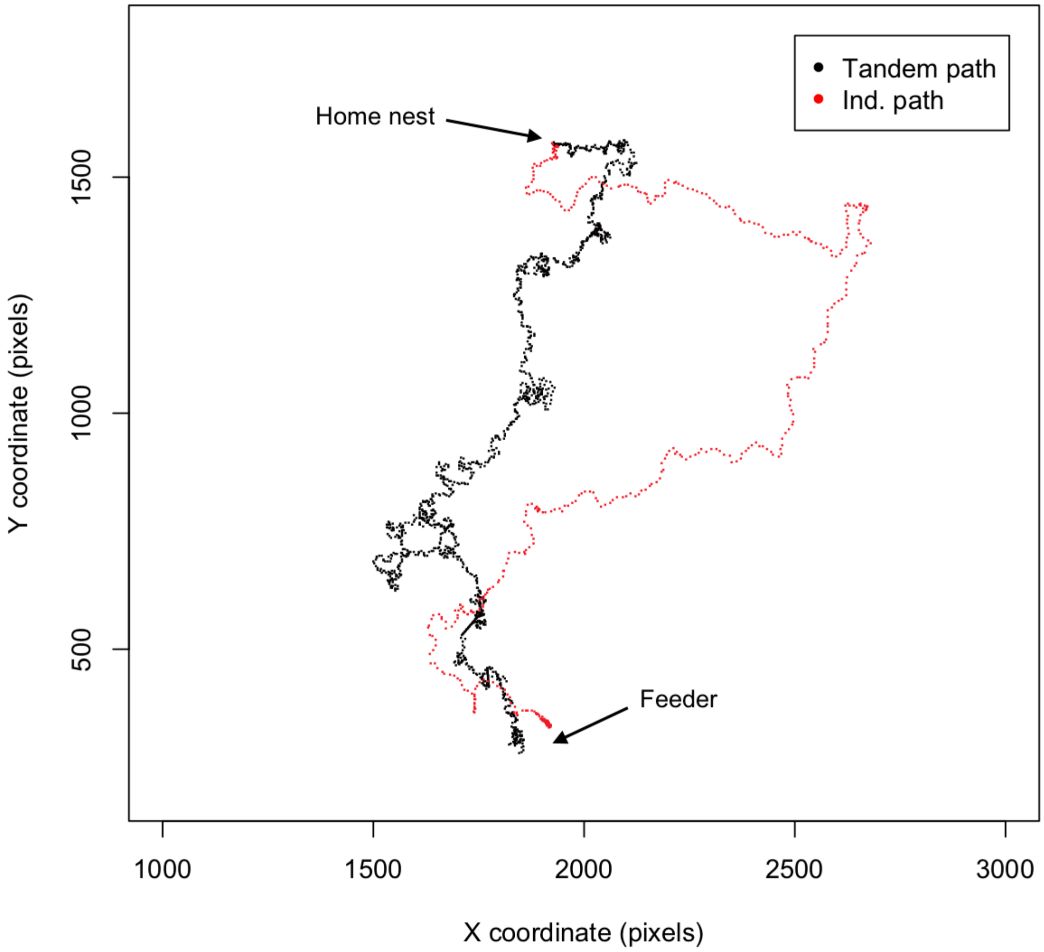


Fig. 4.4. Survival analysis of the proportion of colonies before first tandem run (lost or completed) for food and nest, adjusted by subtracting time of target discovery for each colony’s first tandem run time. The lines show the number of colonies for each treatment prior to a tandem run; the lines decline one step when a colony started a tandem run. Tandem run started significantly earlier in food than nest (Cox proportional hazard model: *Chisq* = 4.57, *p* = 0.032). Mean time of first food tandem run = 16.29 min; mean time of first nest tandem run = 28.71 min.

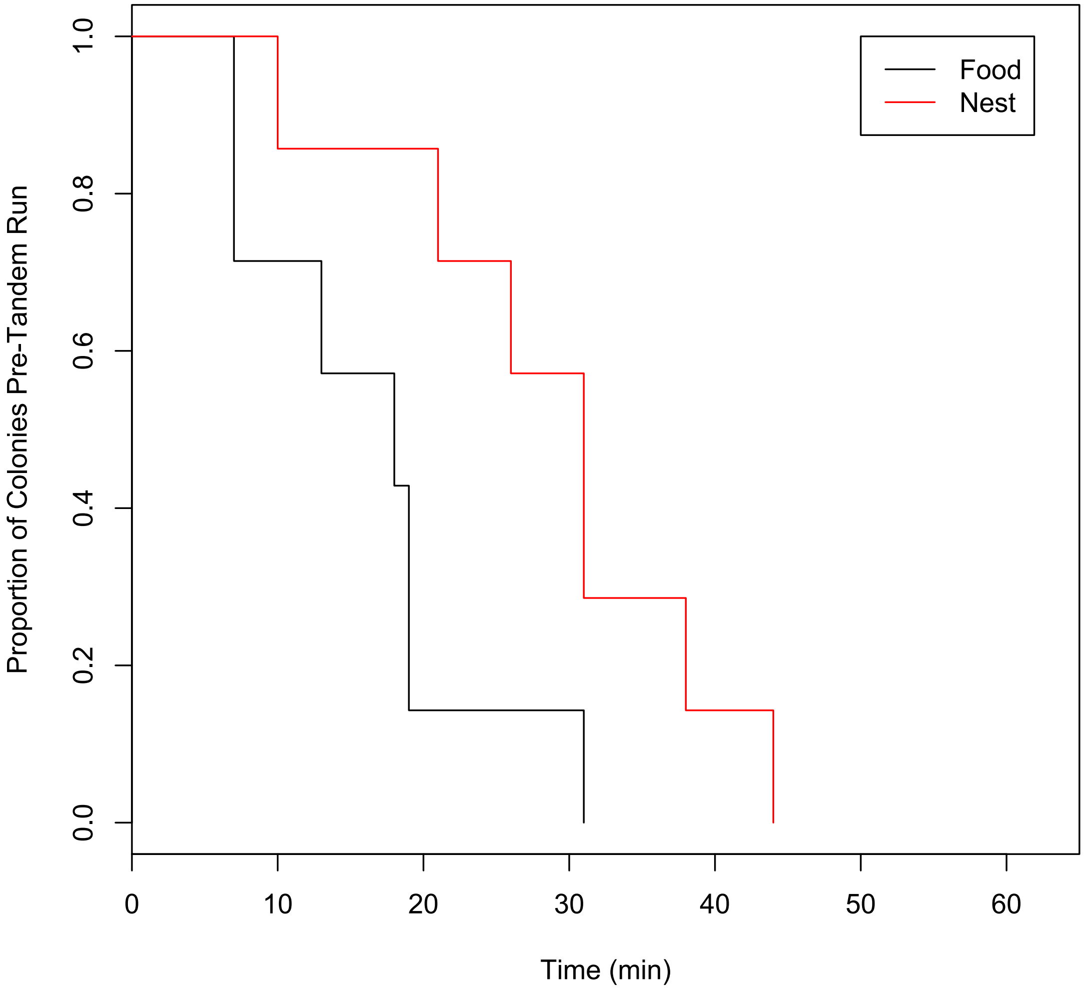


Fig. 4.5. Time of target discovery (min; time since the beginning of trial) by target type. Discovery time for food is 17.71 ± 3.41 min (mean ± SE), while the time for nest is 41.57 ± 6.87 min. Discovery for food is significantly earlier than nest (Cox Proportional Hazard model: *Chisq* = 6.42, *p* = 0.011).

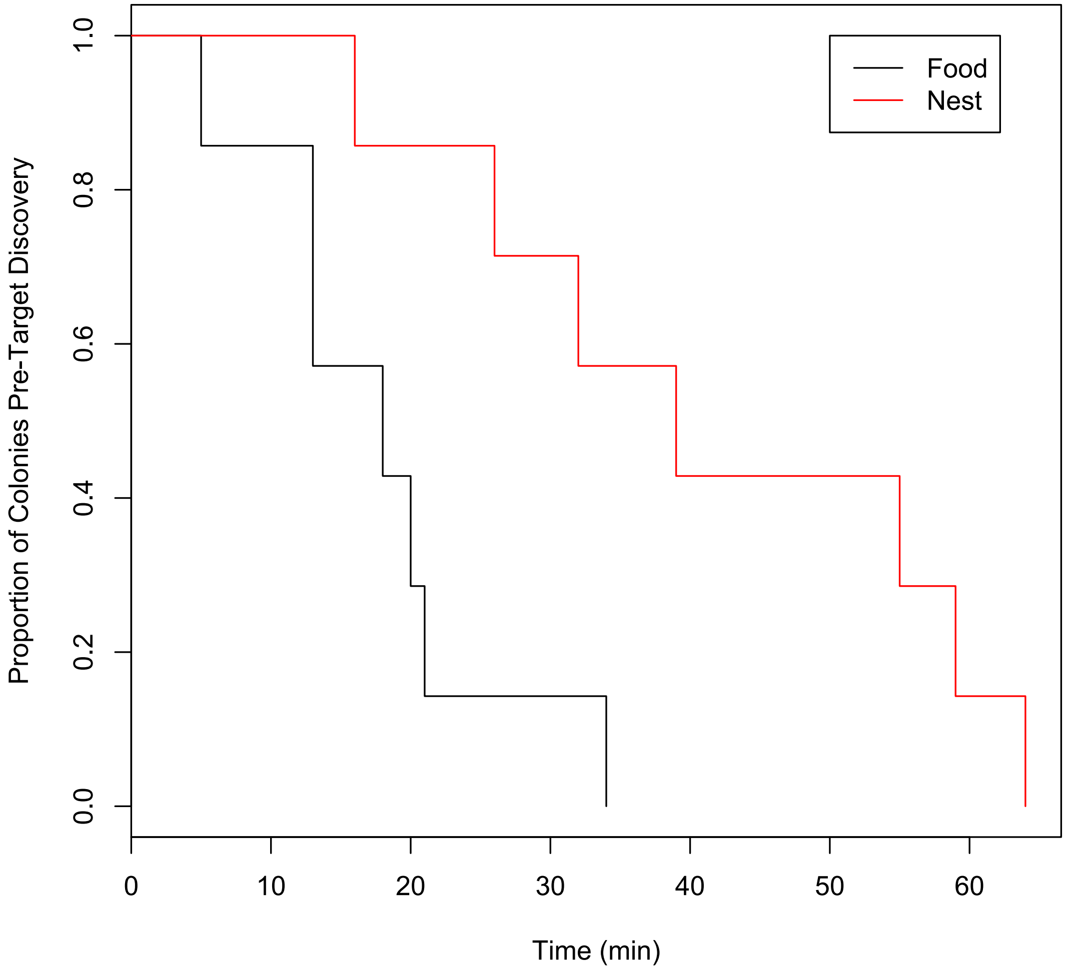


Fig. 4.6. Survival analysis of the proportion of colonies before first completed tandem run for food and nest, adjusted by subtracting time of target discovery for each colony's first completed tandem run time. The lines show the number of colonies for each treatment prior to a complete tandem run; the lines decline one step when a colony started a complete tandem run. The first completed tandem runs started at statistically equal times (Cox proportional hazard model: *Chisq* = 0.99, *p* = 0.32). Mean time of first completed food tandem run = 38.86 min; mean time of first completed nest tandem run = 38.14 min.

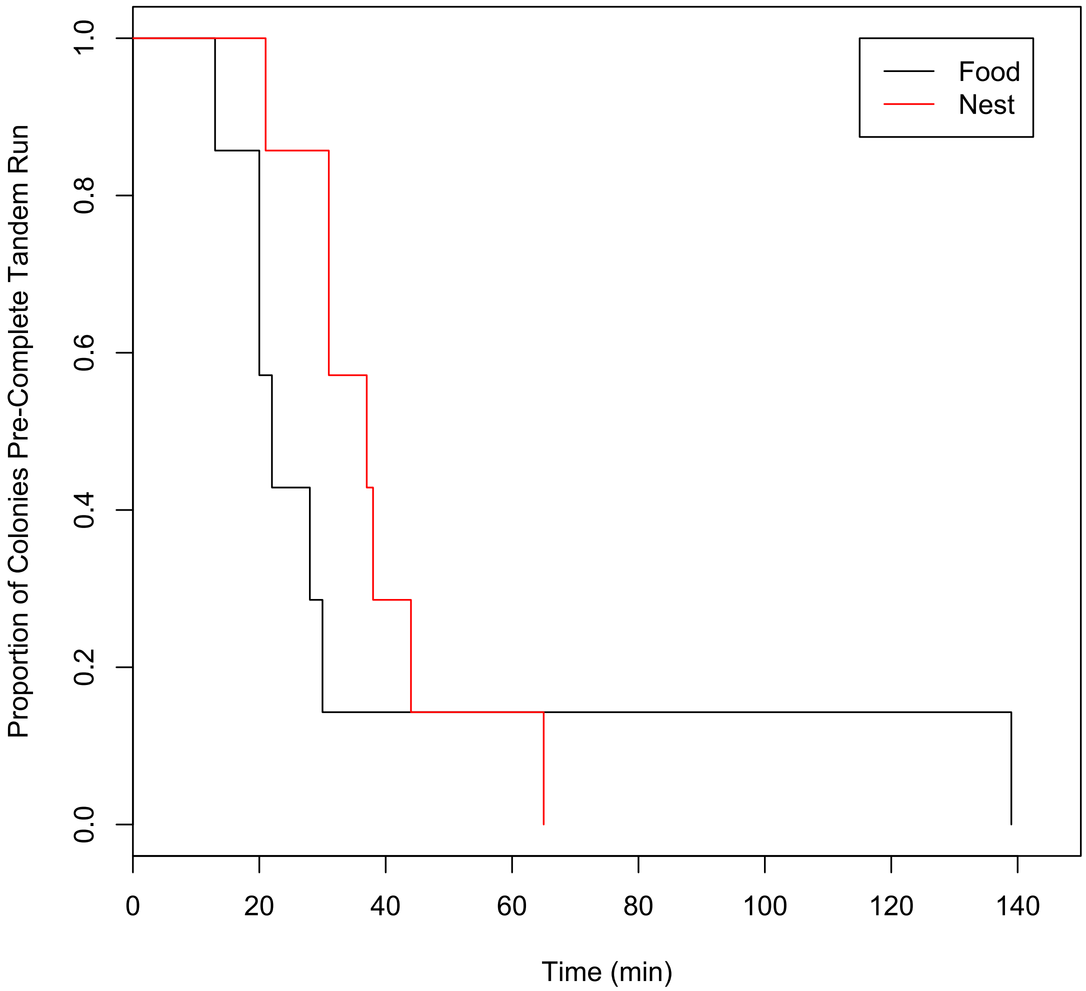


Fig. 4.7. Straightness of paths in food and nest tandem runs. The food tandem paths were not significantly straighter than the nest tandem paths (two-sample *t*-test: $t = 1.51$, $df = 22$, $p = 0.14$). Mean straightness of food tandem paths = 0.35; mean straightness of nest tandem paths = 0.27.

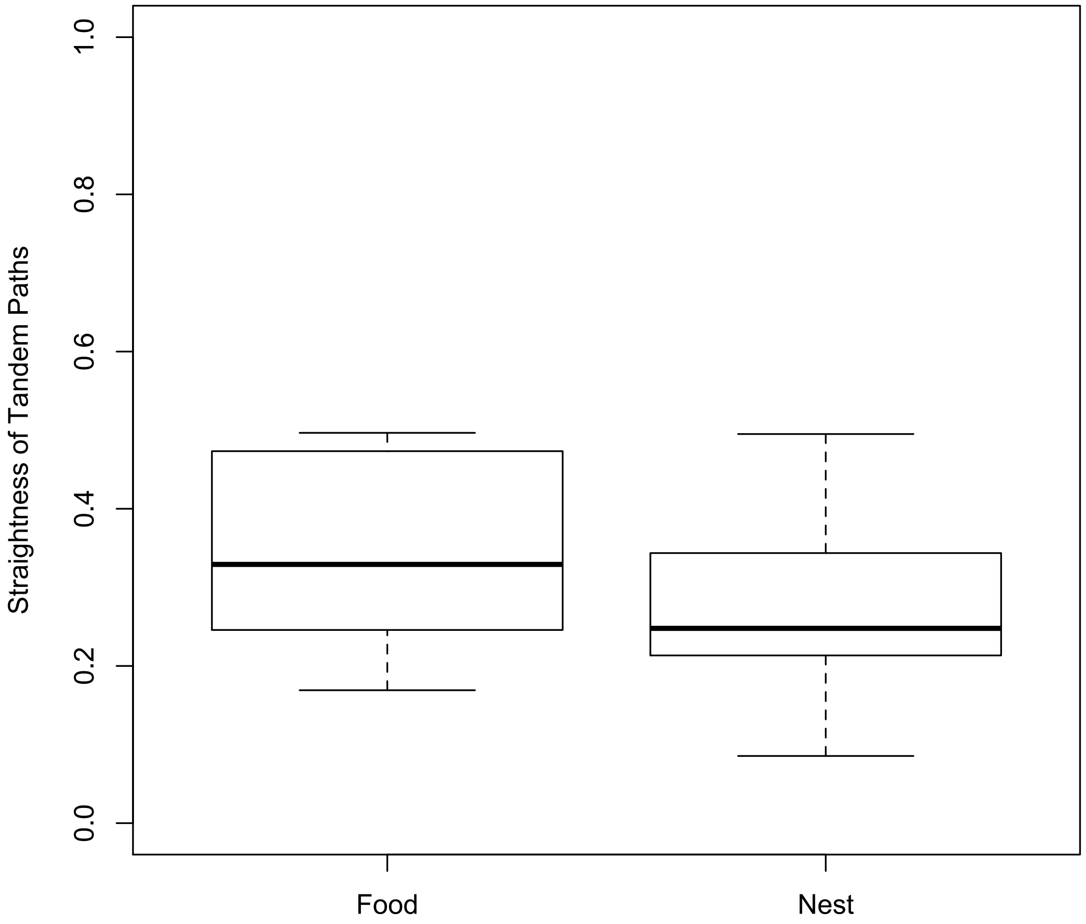


Fig. 4.8. The time (sec) when a tandem pair reaches the target. For food, the mean ± SE is 258.5 ± 29.93 sec, while for nest, the value is 369.58 ± 61.90 sec. This time for nest is longer than that for food, although the difference is not significant (Mann-Whitney U-test: $W = 44$, $p = 0.11$).

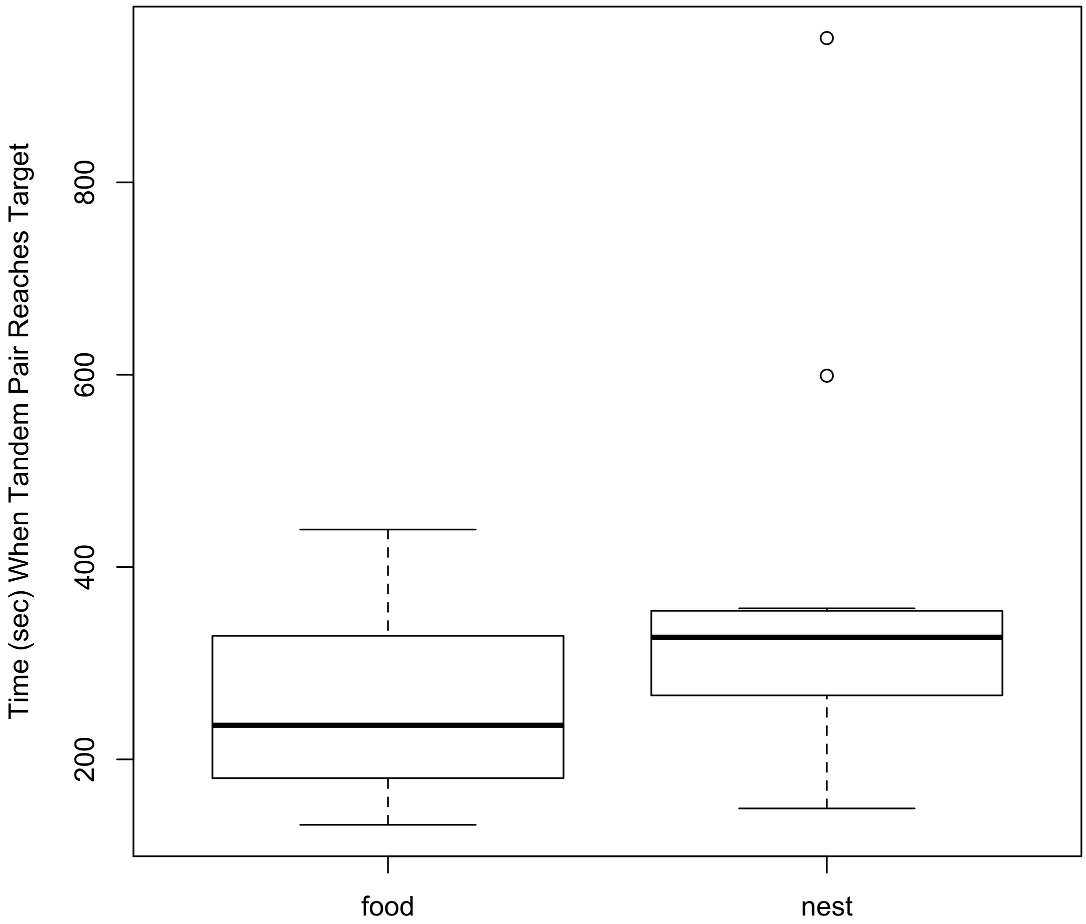


Fig. 4.9. Difference between tandem and follower's independent paths for blocked and control treatments. The differences for the two treatments was statistically indistinguishable (Welch two-sample *t*-test: $t = -0.28$, $df = 13.6$, $p = 0.78$). Mean difference of block = 225.1; mean difference of control = 215.3. The variance for control treatment is significantly higher (Levene's test : $F = 9.04$, $df = 1$, $p = 0.008$). The thick middle line indicates the median, while the lower and upper hinge indicates the 25th and 75th quantile, respectively. The lower whisker indicates the smallest value within 1.5 times the interquartile range below 25th quantile. The upper whisker indicates the largest value within 1.5 times the interquartile range above 75th quantile.

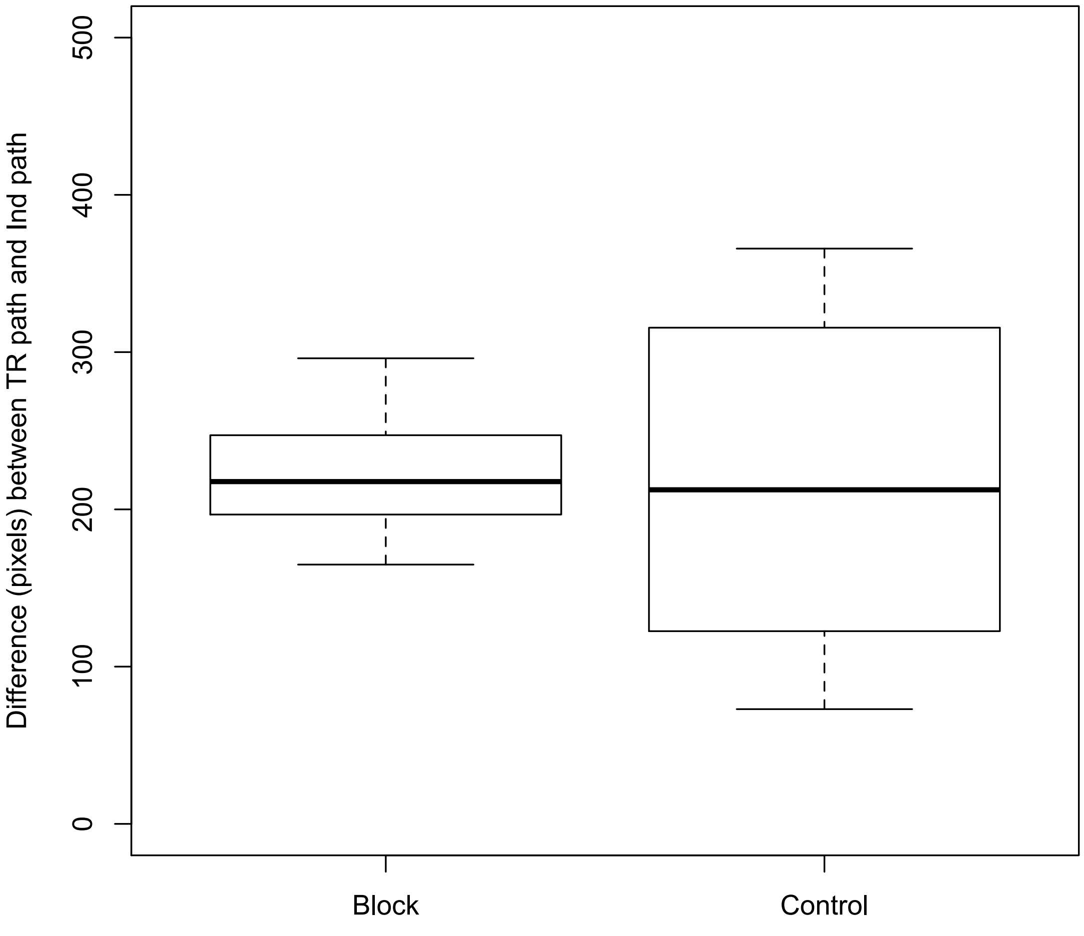


Fig. 4.10. Straightness of path in followers' independent paths for block and control treatments. The independent paths of followers in control treatments were significantly straighter than those in block treatments (two-sample *t*-test: $t = -2.90$, $df = 18$, $p = 0.010$). Mean straightness of block = 0.17; mean straightness of control = 0.36.

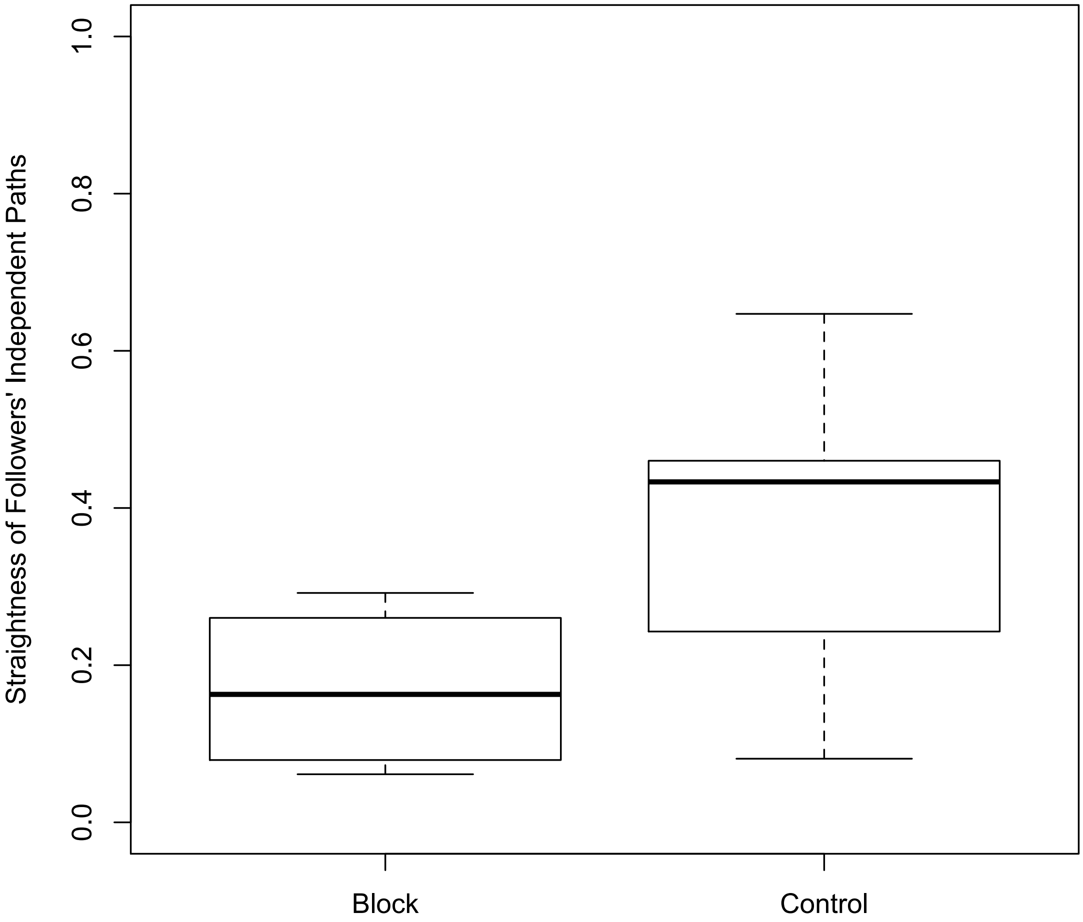


Fig. 4.11. The time (sec) when the follower reaches the target, on its independent path. For block, the mean ± SE is 216.67 ± 42.03 sec, while for nest, the value is 126.18 ± 34.98 sec. This time for block is longer than control, though the difference is not significant (Mann-Whitney U-test: $W = 75$, $p = 0.057$; 1-2 ties).

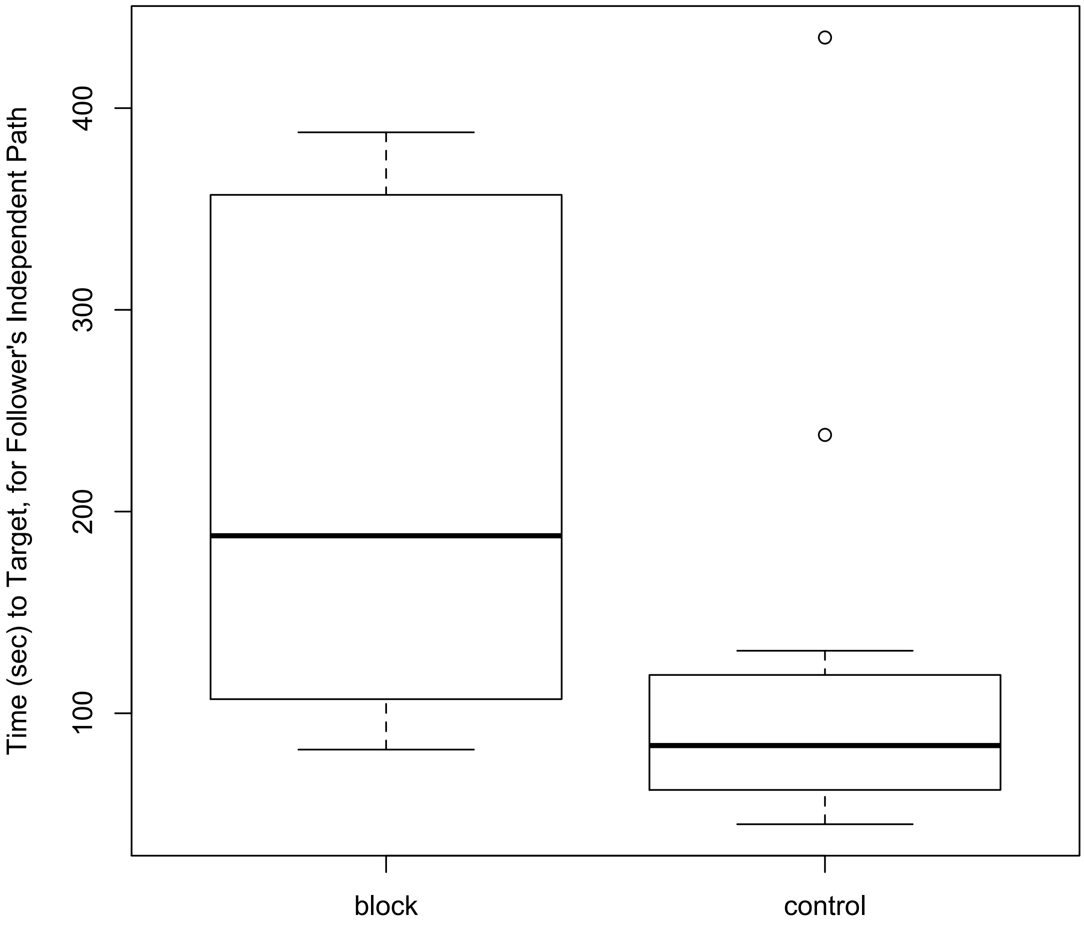


Table 4.1. Proportion of tandem runs that are lost or complete.

	Food	Nest
Lost tandem runs	16	7
Complete tandem runs	11	17
Total	27	24

Fisher's exact test: $p = 0.048$ (favoring food lost rate; odds ratio = 3.44).

CHAPTER 5

CONCLUSION

From my dissertation, I have investigated several things about recruitment in the ant *Temnothorax rugatulus* and how its colonies make decisions collectively. Recruiters bringing nestmates to food and nest behave differently: food recruiters perform the two new behaviors I described (shaking and vigorous antennation) more frequently than nest recruiters (Chapter 2). These differences in behavior are relevant for collective decision making by colonies, because when I present them with a conflict between hunger and nest need, the colonies show some evidence that this poses a tradeoff, and that they allocate their workforce according to the tradeoff (Chapter 3). The way in which colonies spatially allocate their workforce to food and nest could be different as well, because food recruiters have a higher loss rate and start recruiting earlier than nest recruiters, which is consistent with the tuned error hypothesis (Weidenmüller and Seeley 1999). As for recruits arriving at the targets, I do not yet know whether these recruits are able to increase the chance of arriving at the target in the future by repeatedly using the paths that they were led on (Chapter 4).

There are a number of remaining questions relevant to this work. In Chapter 2, since I did not find an effect of shaking or vigorous antennations on the behavior of recipients, a more in-depth investigation is needed to find out whether potential recruits are able to distinguish food recruiters and nest recruiters based on their behavior. Another possibility is that potential recruits can distinguish the recruiters by other means such as sucrose concentration during trophallaxis. Because I presented each target by itself, it is also worth investigating how recruiters and potential recruits in home nest behave when the colony is simultaneously considering food and new nest options.

In Chapter 3, what is the mechanism underlying the allocation in workforce according to the tradeoff hypothesis? Are food recruiters and nest recruiters distinct group of ants in the colony, or do they come from the same pool of recruits? Also, one potential reason why most results do not directly support the tradeoff hypothesis is that nest need was not different enough between high nest need and low nest need colonies. If nest need is sufficiently different between the two levels, will this make the results more supportive of the tradeoff hypothesis?

In Chapter 4, since I did not measure walking speeds of the ants, it would be interesting to see if instantaneous or average speed is different between food and nest tandem runs. Likewise, for the second experiment, are follower ants' speed during independent paths different between block and control treatments? One interesting result on the second experiment was that the deviation of independent paths from tandem paths in control treatments was more variable than that in block treatments. Does greater variation in deviation for control treatments stem more from variation in independent paths, or more from variation in tandem paths?

This dissertation prompts future studies to investigate collective behavior and decision-making in a broader view; not just about one task or a type of resource, but investigating multiple tasks or types of resource. This has been explored in other systems (Visscher 2007; Marting, Wcislo, and Pratt 2018; Arenas and Kohlmaier 2019; Grüter et al. 2018; Gordon 1986), but there are not many studies so far. More in-depth studies in two or more resource types are needed for a better understanding of how collective decisions are made and how colonies resolve tradeoffs among multiple resource types. One could also investigate which resource type is more important for the colony as well. Another interesting aspect to investigate in the future is how colonies spatially allocate their workforce among multiple resource types. The results here could lead to a development of proxies for natural distribution of resources relative to that of other resource types. For example, one could observe a colony of an ant species while it recruits to multiple resource types, measure the recruitment error rate for each type. The recruitment error rate could then be used to deduce which resource type is more sparsely distributed in the area. Overall, these investigations could lead to insights that improve management practices for economically important social insects such as honeybees or invasive red imported fire ants.

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APPENDIX A

SUPPLEMENTARY MATERIALS FOR CHAPTER 2

Table S1. Nest experimental design

Colony ID	First treatment	Second treatment	Third treatment
Colonies A and B	Good nest	Poor nest (no data for colony B)	
Colonies C and D	Poor nest (no data for colony D)	Good nest	
Colonies E and F	Poor nest (no data)	Good nest (no data needed)	Poor nest
Days since last experiment	14-29	14-23	14

Table S2. Comparison of trophallaxis duration and visit duration by quality. The values are mean ± SE.

Food	1 M recruiters ($N = 10$)	0.1 M recruiters ($N = 9$)	Significance	
Trophallaxis (min)	5.01 ± 0.695	4.22 ± 0.663	$t = 0.82$, $df = 17$, $p = 0.43$	Two-sample *t*-test
Nest visit duration (min)	6.34 ± 0.728	6.11 ± 0.801	$t = 0.21$, $df = 17$, $p = 0.83$	Two-sample *t*-test
Nest visit duration, excluding trophallaxis (min)	1.33 ± 0.206	1.89 ± 0.281	$t = -1.63$, $df = 17$, $p = 0.12$	Two-sample *t*-test

Nest	Good nest recruiters ($N = 8$)	Poor nest recruiters ($N = 8$)	Significance	
Nest visit duration (min)	1.70 ± 0.439	1.12 ± 0.167	$W = 41$, $p = 0.38$	Mann-Whitney

Table S3a. Recipients of vigorous antennations in food vs. nest

Behavior	Target quality	Recipients in food, n/N (%)	vs.	Recipients in nest, n/N (%)	P-value, CMH[a]
Trophallaxis	Poor	7/12 (58.3)		1/7 (14.3)	0.0058*
	Good	13/23 (56.5)		1/10 (10)	
Move to the entrance	Poor	2/12 (16.7)		5/7 (71.4)	0.046*
	Good	9/23 (39.1)		6/10 (60)	
Exit nest	Poor	1/12 (8.3)		5/7 (71.4)	0.00036*
	Good	3/23 (13)		6/10 (60)	
Follow a tandem run	Poor	0/12 (0)		1/7 (14.3)	0.51
	Good	1/23 (4.3)		1/10 (10)	

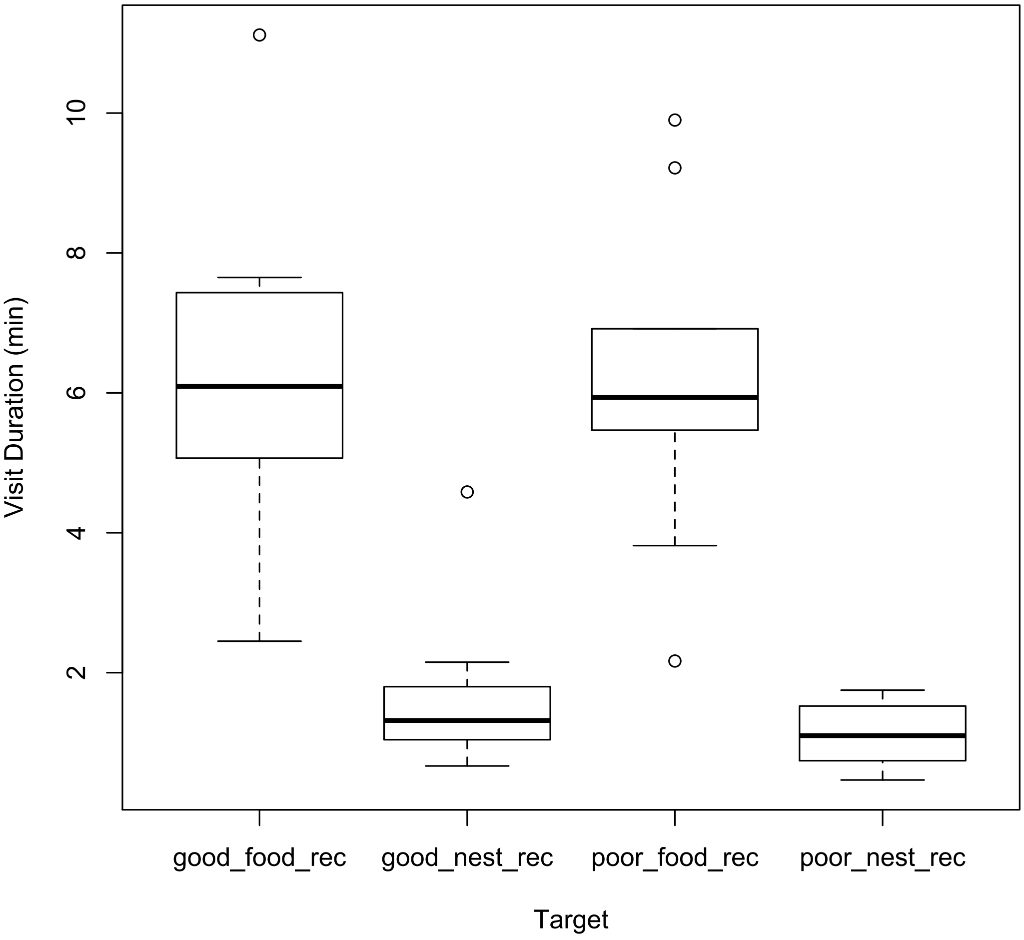
a. CMH = Cochran-Mantel-Haenszel X^2 test, testing for difference between recipients in food and recipients in nest, while controlling for target quality; significance level $*p < 0.05$

Table S3b. Controls of vigorous antennations in food vs. nest

Behavior	Target quality	Controls in food, n/N (%)	vs.	Controls in nest, n/N (%)	P-value, CMH[a]
Trophallaxis	Poor	3/6 (50)		0/7 (0)	0.031*
	Good	5/9 (55.6)		1/7 (14.3)	
Move to the entrance	Poor	2/6 (33.3)		5/7 (71.4)	0.37
	Good	4/9 (44.4)		4/7 (57.1)	
Exit nest	Poor	1/6 (16.7)		5/7 (71.4)	0.2
	Good	4/9 (44.4)		4/7 (57.1)	
Follow a tandem run	Poor	1/6 (16.7)		0/7 (0)	0.15
	Good	3/9 (33.3)		0/7 (0)	

a. CMH = Cochran-Mantel-Haenszel X^2 test, testing for difference between controls in food and controls in nest, while controlling for target quality; significance level $*p < 0.05$

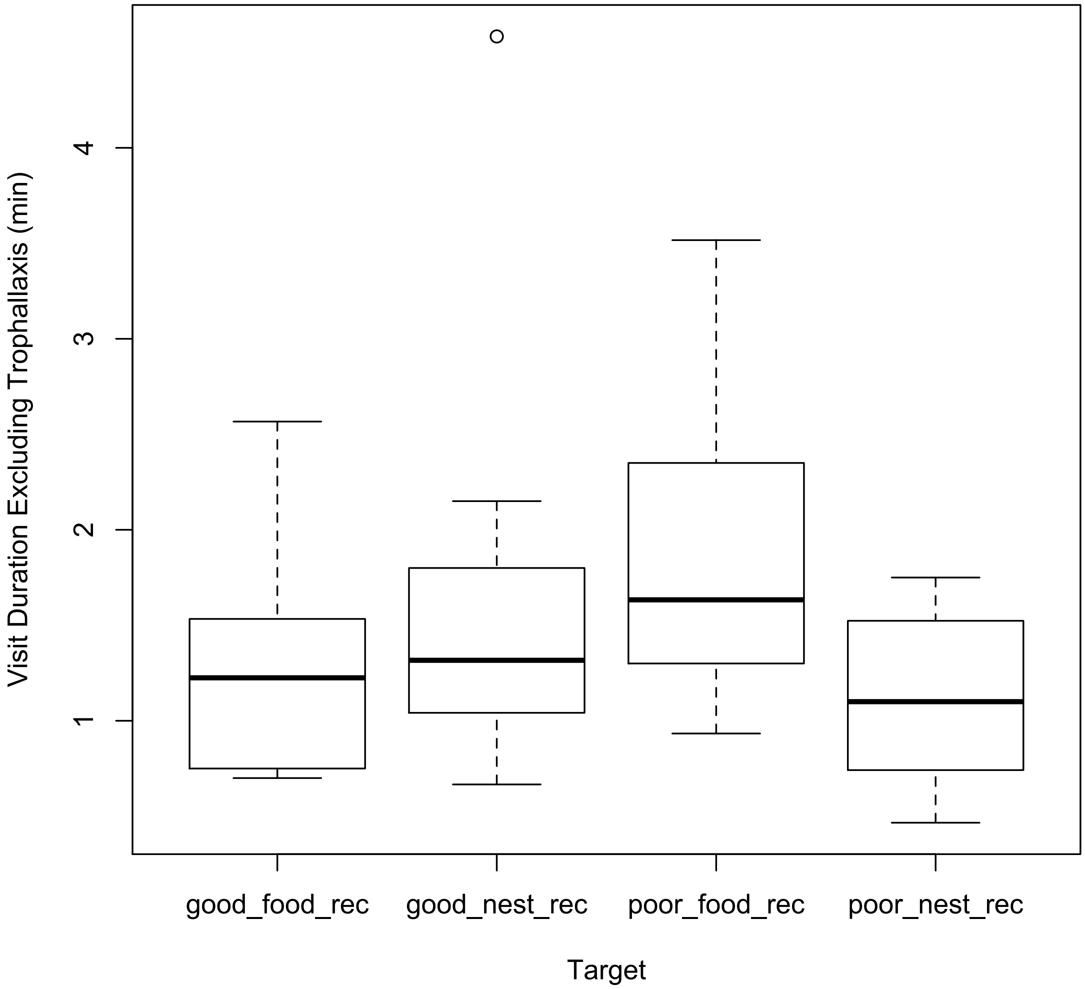
Online Resource 1:



The effect of target on visit duration (with trophallaxis) is significant (Kruskal-Wallis; *Chisq* = 24.4, *df* = 3, *p* < 0.0001).

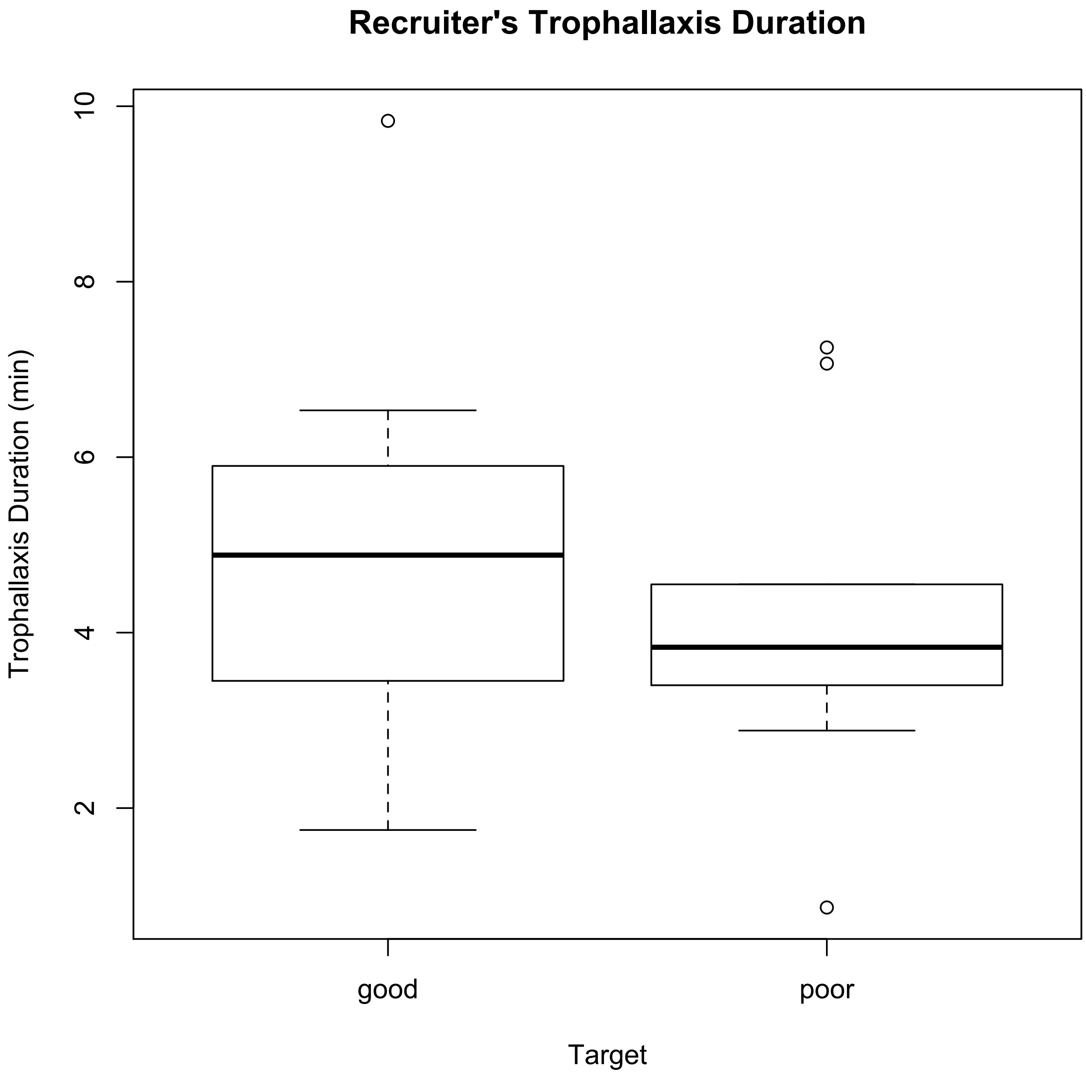
Dunn's posthoc test (Dunn 1961; Dunn 1964; Holm 1979; Signorell et mult. al. 2017) shows:
Good food is significantly greater than good nest (*p* = 0. 0033),
and poor food is significantly greater than poor nest (*p* = 0.0018.)

Online Resource 2:



The effect of target on visit duration (without trophallaxis) is not significant (Kruskal-Wallis; *Chisq* = 4.5, *df* = 3, *p* = 0.22).

Online Resource 3:



The duration of trophallaxis between good and poor food recruiters is not significantly different (Two-Sample *t*-test; $t = 0.82$, $df = 17$, $p = 0.43$).

[Online Resources 4 and 5 are deleted because they are videos].

Online Resource 6: *Shaking displays: Poisson regression*

The simplest and best-supported Poisson regression model included only a main effect of target type, with no main effect of quality and no interaction between target type and quality. Analysis of deviance showed that the model with only target type was statistically indistinguishable from the full model with main effects and their interaction ($p = 0.37$) and from a model with only main effects ($p = 0.22$). In contrast, a model with only target quality explained significantly less variation than either the full model ($p = 0.016$) or the model with only main effects ($p = 0.0052$).

Online Resource 7: *Vigorous antennations: Poisson regression*

The best-supported Poisson regression model was the full model including target type, food quality, and their interaction. That is, the full model explained significantly more variation than models with type only ($p = 0.014$), quality only ($p = 0.00014$), or both type and quality but no interaction ($p = 0.015$).

Online Resource 8: Quasi-Poisson on the duration of trophallaxis and move to entrance for recipients of shaking:

Recipients of shaking displays: statistical procedure on the duration of trophallaxis

For trophallaxis, the best-supported quasi-Poisson regression model included only the effect of receiving shaking vs. control, which was not significant (p = 0.79). Analysis of deviance showed that the model with only shaking vs. control was not statistically distinguishable from the full model with shaking vs. control, food quality and their interaction (p = 0.27), and from a model with only main effects (p = 0.21). Since the three models are not statistically different from each other (p = 0.34 for the full model vs the model with only main effects), I tried removing the interaction from the full model, and found no significant factors. I removed food quality from the model with only main effects, and again found no significant factor. Also, the model with only food quality (food quality p = 0.26) was not statistically distinguishable from the full model with interaction (p = 0.62) and from the model with only main effects (p = 0.83). Finally, when I separately tested the two food qualities, I found no effect of shaking vs. control on the duration of trophallaxis for either good food (p = 0.88) or poor food (p = 0.31).

Recipients of shaking displays: statistical procedure on the duration of moving to entrance

For the duration of moving to entrance, the best-supported quasi-Poisson regression model included only the effect of receiving shaking vs. control, which was not significant (p = 0.15). Analysis of deviance showed that the model with only shaking vs. control was not statistically distinguishable from the full model with shaking vs. control, food quality and their interaction (p = 0.40), and from a model with only main effects (p = 0.88). Since the three models are not statistically different from each other (p = 0.18 for the full model vs the model with only main effects), I tried removing the interaction from the full model, and found no significant factors. I also removed food quality from the model with only main effects, and again found no significant factor. Also, the model with only food quality (food quality p = 0.94) was not statistically distinguishable from the full model with interaction (p = 0.10) and from the model with only main effects (p = 0.11). Finally, when I separately tested the two food qualities, I found no effect of shaking vs. control on the duration of moving to entrance for either good food (p = 0.087) or poor food (p = 0.96).

Online Resource 9: *Poisson for shaking, analyses separated by quality effects and then by context effects, each effect by its own.*

Quality effect only

When analysis was done with quality as the only predictor, recruiters in poor targets and those in good targets performed shaking at an equal level (*p* = 0.18).

Context effect only

When analysis was done with context as the only predictor, food recruiters did significantly more shaking than nest recruiters (*p* = 0.0027).

Context effect within each quality

In poor recruiters, those in food performed more vigorous antennation than those in nest (*p* = 0.049).

In good recruiters, those in food performed more vigorous antennation than those in nest (*p* = 0.028).

Quality effect within each context

In food recruiters, those in poor food and those in good food performed shaking at an equal level (*p* = 0.34).

In nest recruiters, those in poor nest and those in good nest performed shaking at an equal level (*p* = 0.34).

Online Resource 10: *Poisson for vigorous antennation, analyses separated by quality effects and then by context effects, each effect by its own.*

Quality effect only

When analysis was done with quality as the only predictor, recruiters for good targets did significantly more vigorous antennation than recruiters for poor targets ($p = 0.043$).

Context effect only

When analysis was done with context as the only predictor, food recruiters did significantly more vigorous antennation than nest recruiters ($p = 0.022$).
- Poisson was overdispersed at 0.05, so used quasi-Poisson (dispersion parameter: 3.12)

Context effect within each quality

In poor recruiters, those in food performed more vigorous antennation than those in nest ($p = 0.000058$).

In good recruiters, those in food performed more vigorous antennation than those in nest ($p = 0.044$).

Quality effect within each context

In food recruiters, those in poor food and those in good food performed vigorous antennation at an equal level ($p = 0.63$).

In nest recruiters, those in good nest did significantly more vigorous antennation than those in poor nest ($p = 0.0062$).

Online Resource 11:

I counted the number of vigorous antennations or shaking displays each recipient received, and found most to be about one. The average number of vigorous antennation that each recipient of vigorous antennation received across treatments is 1.1 (ranges from 1 to 3; six ants with >2 instances received). The average number of shaking that each recipient of shaking received across treatments is 1.3 (ranges from 1 to 3; five ants with >2 instances received).