

Social interactions differ in their impact on foraging decisions

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Animals rely on both personal and social information when making decisions. To acquire social information, animals interact with other individuals. However, not all interactions are the same. The type of interaction (e.g. affiliative or agonistic) and the state of the individual one interacts with may impact the information provided. Here we asked whether the decisions of ants to forage are determined by individual or social information and whether the type of social interaction experienced impacts these decisions. We found that foragers of the Argentine ant, *Linepithema humile*, relied predominantly on local interactions of particular types when deciding whether or not to continue foraging. Specifically, the time a forager spent in the nest was affected by the proportion of trophallactic interactions it experienced but not by other types of interactions. Furthermore, latency to leave the nest was only affected by the proportion of trophallactic interactions with hungry ants and not by other interactions or by personal information. Finally, global colony hunger level did not affect a forager's decision to continue foraging. Thus, the type of interaction and the state of the individual one interacts with impact decision making. Therefore, when examining the emergence of collective outcomes from local interactions, it is important to consider the nature of these interactions and not only their rate or quantity.

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Animals constantly use information to make decisions, such as when and where to forage or find shelter and with whom to mate. To make an accurate decision, animals use information that can be acquired from personal experience (personal information) or based on social interactions with other individuals (social information) (Wagner & Danchin, 2010). Acquiring personal information can be beneficial if social information is not reliable (Kendal et al., 2005), but it can also be costly because of the time it takes to acquire and the potential associated threats (Smit & van Oers, 2019; Webster & Laland, 2008). Social interactions can be an efficient way to gain information (Bonnie & Earley, 2007), but the information might not be reliable because, for example, the individuals providing information might differ in the accuracy of information they possess (Aguinaga et al., 2021; Danchin et al., 2004; Giraldeau et al., 2002; Heinen & Stephens, 2016).

The nature of social interactions determines future actions. When animals interact, they gain information, for example about the location (Harel et al., 2017) and quality (Coolen et al., 2005) of food, social status (Hobson et al., 2021) and presence of predators (McRae, 2020). Based on such social information, animals often

change their behaviour (Battesti et al., 2012). Different types of interactions provide different information, for example, an agonistic encounter may provide information about social status (Hobson et al., 2021), while a grooming interaction might provide information about the parasite load of groupmates (Akinyi et al., 2013; Duboscq et al., 2016). Therefore, the response of an individual to each type of interaction will depend on the nature of the interaction, for example, flee from a fight or follow an informed individual to food. Furthermore, with whom one interacts can influence the type of information received. Individuals differ in their experience, age, physiological state, and so forth, and these differences may affect the type of information they convey when interacting. For example, juveniles provide less accurate information about predation threat than adults, because of differences between juveniles and adults in life experience (Ramakrishnan & Coss, 2000; Seyfarth & Cheney, 1986). Thus, the response of animals to social information from different individuals may depend on who the information comes from and how reliable it is (Blumstein & Daniel, 2004; Hare & Atkins, 2001).

Social insects live in colonies that operate as collective units and, therefore, they rely heavily on social interactions for gaining information. The collective behaviour of social insects emerges from social interactions (Gordon, 2010; Seeley, 1995). Each individual responds to local interactions, without information about the

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global state of the colony. Interaction rates regulate collective behaviours such as foraging (Cook et al., 2020; Pinter-Wollman et al., 2013) and deciding where to nest (Seeley, 2010). Despite the importance of social interactions for colony function, there has been little research on how a single species uses different types of interactions to provide different types of information. Social insects engage in different types of interactions, such as food sharing, antennation, aggression, and so forth, and each of these interactions provides different information. Sometimes, only the combination of multiple types of interactions can uncover important social information (Gadagkar et al., 2022; Sharma et al., 2022).

An important collective behaviour that ant colonies engage in, and that requires gathering information to reach important decisions, is collective foraging. Certain individuals in a colony act as foragers that leave the nest to collect food, while others remain in the nest to perform other tasks, such as care for the queen and brood (Gordon, 1989, 1996). How a forager decides whether or not to forage (i.e. whether the colony is hungry) has been the topic of much research. Foragers often rely on interactions with nestmates (Gordon, 2010), the presence of larvae (Ulrich et al., 2016), their own crop load (Howard & Tschinkel, 1980; Wallis, 1964) and the waiting time between arriving at the nest and offloading their food (Seeley, 1989) to determine whether foraging is required. Harvester ants use the rate at which they encounter successful foragers (ants carrying seeds) to determine whether to continue foraging (Greene et al., 2013; Pinter-Wollman et al., 2013). In

carpenter and *Formica* ants, foraging decisions are regulated by the crop load of foragers and the rate at which foragers unload their crops (Greenwald et al., 2018; Wallis, 1964). Argentine ants can regulate the nutrients on which they forage based on colony need (Csata et al., 2020), even in high-risk environments (Barbee & Pinter-Wollman, 2022).

While past work on ant foraging decisions has focused on the role of the odour (Greene et al., 2013) or nutritional value (Csata et al., 2020) of food in foraging decisions, here we focus on the type of interactions and information (personal or social) that foragers use to determine the hunger of a colony. Furthermore, we expand past examinations of the impact of interaction rate on foraging decisions to include interaction rates of multiple types of interactions. Specifically, we hypothesized that the type of social interaction (antennation, mouth-to-mouth, trophallaxis), the state of the ant encountered (satiated or hungry) and individual information (time spent regurgitating) play different roles in determining the decision of a forager to continue foraging and bring more food to the colony.

METHODS

Colony Collection and Maintenance

We collected eight groups of Argentine ant (*Linepithema humile*) workers and queens from the UCLA Botanical Gardens and from the

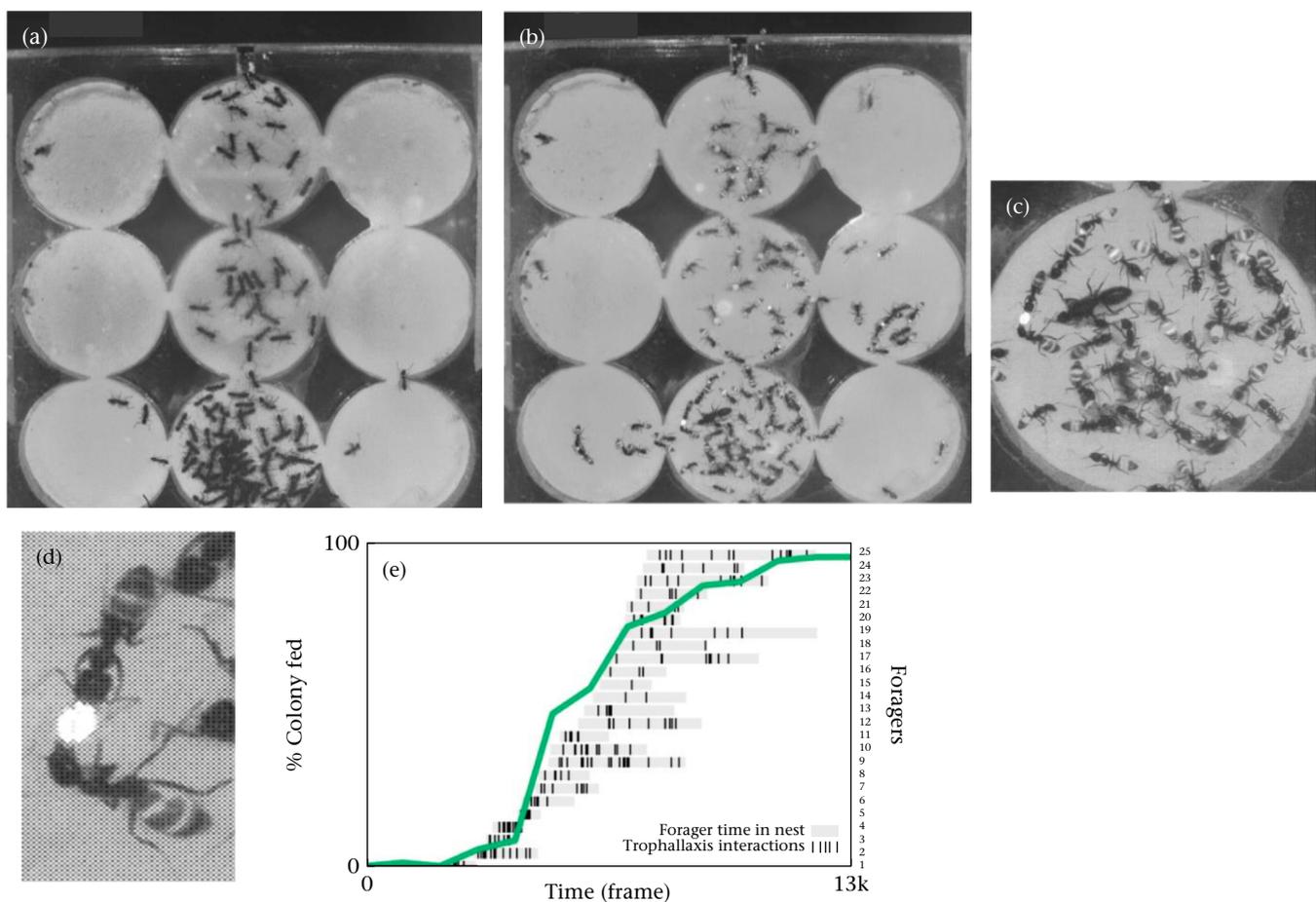


Figure 1. Imaging ants' food content. A colony (workers and queen) in their nest (a) before and (b) after feeding on fluorescently labelled food. (c) Close-up view of the nest chamber with the queen showing the fluorescently labelled food in the ants' abdomens. (d) Close-up view of trophallaxis between two workers; the food being exchanged is visible between the two workers. (e) Tracking trophallaxis events (black tick marks) of returning foragers (rows, time in nest of each forager is indicated in grey) overlaid on the percentage of the colony that contained food (green line) over time (frames). Percentage of colony fed was calculated as the amount of food in the colony at a given time (total fluorescence in a frame) in relation to the amount of food in the colony at the end of the experiment (total fluorescence in the last frame).

sidewalk outside Temescal Canyon State Park, Los Angeles. To ensure groups contained a mixture of individuals from different age and tasks groups, we collected ants from foraging trails and from the nest interior by flooding the nest entrance and aspirating the escaping individuals. Immediately following collection, we placed the eight groups, each containing 200 workers, approximately 50 brood and one queen, in plastic boxes ($20 \times 9.7 \times 9.8$ cm). The walls of the plastic boxes were coated with Fluon to prevent ants from escaping. Each box contained a nest made of Plexiglas that had a 3×3 grid of interconnected circular chambers (2.7 cm diameter \times 2 mm high), with a single entryway (2×4 mm) from the upper middle chamber (Fig. 1a, b). The floor of the nest was filled with moistened plaster and the nest was wrapped in foil to maintain a dark interior. Following introduction into the box, the ants moved themselves into the nest. To provide a constant water source, we placed a vial filled with water and plugged with a cotton ball to allow the water to wick through the cotton but not spill. We stored the colonies in an incubator with constant temperature (25 °C) and humidity (50%) with a 14:10 h light:dark cycle. Before we began observations of foraging behaviour, we starved colonies for 14 days but provided water ad libitum to ensure that colonies were not dehydrated. This starvation duration represents the lower bounds used in similar experiments (2–3 weeks: Baltiansky et al., 2021; 3–5 weeks: Greenwald et al., 2018; 2–8 weeks: Greenwald et al., 2015) and in other starvation experiments in ants (e.g. 20 days: Kwapich & Tschinkel, 2015; 14 days: Shaffer et al., 2013) but slightly longer than is typically used to motivate foraging in other *L. humile* studies (~5 days: Csata et al., 2020; Poissonnier et al., 2019; Reid et al., 2011). We chose to extend this species-typical period of starvation to minimize the quantity of lingering sugar solution in the crops of the ants because it would have been invisible to our fluorescence-based detection system and might have influenced our results (detailed below). At the end of starvation, all brood had been cannibalized or died, so at the time of the experiment, colonies lacked brood.

Recording Colony Behaviour

To determine which ants were fed and to track food exchange, we fed the starved colonies with sugar water that was fluorescently dyed and videorecorded the ants' activity inside the nest during feeding. Twenty minutes before introducing the food and starting the recording, we removed the foil from the nest to allow the colonies to acclimate to the lighting. We introduced food to the starved colony by replacing the water vial with a glass vial containing 1 ml of 1 M sucrose solution with 5 mg of fluorescein (FITC-F1300, Invitrogen, ThermoFisher Scientific, Waltham, MA, U.S.A.; absorption 490 nm/emission 514 nm). We began filming the colony inside the nest within 1 min of introducing the food. All filming was performed through the clear lid of the box to prevent ants' escape and avoid changes to the within-nest airflow. We used Royal Blue Luxeon Rebel Color LED lights (peak wavelength = 447.5 nm; Luxeon Star LEDs, Randolph, VT, U.S.A.) to illuminate the nest during recording and to excite the FITC in the food. We filmed the nest from above with a CMOS colour camera (FLIR Chameleon3 3.2 MP Color USB3 Vision, Sony IMX265) fitted with a Tamron lens (M118FM08, 8 mm, 1/1.8 inch) and a 540 nm Semrock filter to capture the FITC emission. The nest was recorded at 10 frames/s for 20 min using the 'Micro-Manager' image capture software (Edelstein et al., 2014). The camera did not capture the activity outside the nest (i.e. at the food source), however, the food content of ants returning to the nest was visible through their abdomens (Fig. 1b–d) so we could infer that they visited the food.

Forager Behaviours

We manually tracked the behaviour of every forager returning to the nest with food using a custom MATLAB (Mathworks Inc., Natick, MA, U.S.A.) script. The script allowed observers to record the time and location of behaviours by placing the computer mouse cursor on the location of a behaviour in a frame on the computer screen and clicking a particular letter coded for each behaviour. The behaviours recorded for each focal forager allowed us to determine how long it spent in the nest before it decided to continue foraging and the amount of personal and social information it obtained while in the nest. To determine the time a forager remained inside the nest, we recorded the frame at which a forager (1) entered and (2) exited the nest. To determine the 'personal information' that a forager obtained (i.e. information based on its own experience without interacting with any nestmates), we recorded the start and end of food regurgitation. We defined food regurgitation as a forager standing still with food visibly resting in its mandibles but with no recipients present. Foragers do not interact with any other individuals during regurgitation; they remain stationary and display their food, presumably waiting for it to be unloaded. To determine the 'social information' that a forager obtained (i.e. information based on interactions with nestmates), we recorded three types of interactions: (1) antennation, defined as one of the ants orienting towards the other and tapping that ant at least once with its antenna; (2) the start and end of trophallaxis, defined as the exchange of liquid food between two individuals that lasted at least 0.5 s (Fig. 1d); (3) brief mouth-to-mouth contact, defined as two ants contacting each other using their mandibles for less than 0.5 s and not exchanging food. For each interaction, observers noted whether or not the abdomen of the nonfocal ant was fluorescent to determine whether the forager interacted with a hungry (no fluorescence) or fed (fluorescent) nestmate. All behaviours were recorded for each forager's entire duration inside the nest. Because ants were not individually marked and the food outside the nest was not filmed, a forager that left the nest and returned was considered a new individual. However, because we set out to ask what underlies a decision to continue foraging after a forager returns to the nest, our unit of analysis was a return trip, rather than a particular forager. Thus, our inability to distinguish among foragers did not affect our ability to examine foragers' decisions after they returned to the nest with food. Because the behavioural record of late-returning foragers was censored (i.e. the video recording stopped before the forager left the nest), we only tracked foragers returning up until the rate of food increase began to slow (Fig. 1e) or until 1500 frames before the end of the video, whichever came first.

Forager Decisions

To quantify the decisions of foragers to continue foraging after visiting the nest, we used two variables: 'time spent in the nest' and 'latency to leave nest after the last interaction'. Time spent in the nest was the number of frames from the first frame we began tracking the forager inside the nest to the last frame the forager was tracked. Latency to leave the nest after the last interaction was quantified as the number of frames that elapsed between the last time a forager had any interaction (of any type) with another ant until it left the nest. For foragers that did not leave the nest, we used the end of the movie as the end point. In 147 cases of the 1412 returns of foragers that we tracked, the forager did not interact with any other ants while in the nest before it left or before the video ended. These 147 cases were not included in the analysis of the latency to leave the nest after the last interaction.

Data Analysis

To determine whether the decision of a forager to continue foraging was affected by different types of social interactions, the state of the ant encountered or individual information, we used generalized linear mixed models (GLMM). The response variable was either time spent in the nest or latency to leave the nest after the last interaction. To examine the relationship of these response variables with the absolute number of social interactions, we performed two statistical models (one for each response variable) in which the independent variables (fixed effects) in both models included the number of trophallaxis, antennation or mouth-to-mouth interactions with a fed or hungry individual. In addition, we included the number of regurgitation events as a fixed effect in the models as a proxy for individual information. We further included the time at which the ant entered the nest as a fixed effect to account for colony satiation, which increased over time (Fig. 1e). Finally, we included colony identity (ID) as a random effect to account for potential variation among colonies.

We further examined the effect of the proportion of different interactions on time spent in the nest or latency to leave the nest after the last interaction because ants might not rely on the absolute number of interactions but rather on the relative number of each type of interaction they experience. We summed all interaction types (trophallaxis, antennation, mouth-to-mouth with fed and hungry ants) for each tracked forager and divided the number of interactions of each type by this sum to get the proportion of each interaction type relative to all the interactions that each forager experienced. We then ran two GLMMs with either time spent in the nest or latency to leave the nest after the last interaction as the response variable and the proportion of trophallaxis, antennation or mouth-to-mouth interactions with a fed or hungry individuals as well as the number of regurgitation events and the time at which the forager entered the nest as fixed effects. We included colony ID as a random effect in the model.

We ran the GLMMs in R (R Core, 2014) using the 'glmer()' function in the 'lme4' package (Bates et al., 2015) and used the 'Anova()' function from the 'car' package (Fox & Weisberg, 2019) to determine the confidence of our estimates using an analysis of deviance. All data and analysis code can be found in the Supplementary material.

Ethical Note

This work was conducted in accordance with the ASAB/ABS Guidelines for the use of animals in research. Ants are invertebrates and do not require special institutional permissions for experimentation. We handled ants with extreme care. We used an aspirator to collect the ants to minimize ant mortality during collection. No invasive methods were used during the experiments, which involved videorecording ants' behaviour. Ants were starved before the experiments to motivate foraging behaviour.

We followed similar protocols to those used in other studies (see above). Specifically, the starvation period in our experiment was chosen to prevent any queen mortality or above-average mortality of adult workers while providing a sufficiently robust experimental effect while minimizing the number of colonies needed in the study. After the experiments, we kept the ants in the laboratory and provided them with food ad libitum until they died naturally.

RESULTS

We tracked 1412 forager returns to the nest across eight colonies. Most types of interactions positively corresponded to the time a forager spent in the nest, but the number of interactions with hungry individuals was a better predictor of a forager's latency to leave the nest after its last interaction than were other interactions. Interestingly, forager decisions were most impacted by the proportion of trophallaxis interactions they experienced rather than the proportion of other types of interactions.

As expected, the number of interactions of all types, except for antennations with hungry ants, increased with the amount of time a forager spent in the nest (Appendix, Table A1, Fig. A1). However, the amount of time a returning forager spent inside the nest was positively related to the proportion of its trophallaxis interactions relative to all other interactions but not to the proportion of other interaction types (Table 1, Fig. 2). Furthermore, personal information (regurgitation) played an important role in determining a forager's duration in the nest, with duration in the nest increasing with the number of regurgitation events (Table 1, Fig. 3a). When considering the effect of the proportion of interactions on a forager's time spent in the nest, we did not detect a significant effect of the time at which a forager returned to the nest, a proxy for colony satiation (Table 1). However, when considering the absolute number of interactions, there was a very small positive but significant effect of the time at which a forager returned to the nest on a forager's duration in the nest (Appendix, Table A1, Fig. A2a). The random effect colony ID explained only 4.6% of the variance in the statistical model of interaction proportions and 8% in the model of absolute number of interactions.

A forager's latency to leave the nest after its last interaction was positively affected by the proportion of trophallaxis interactions it had with hungry ants (Table 2, Fig. 4) and by the absolute number of trophallaxis interactions it had with fed or hungry ants (Table 3, Appendix, Fig. A3). The number of regurgitations, a proxy for individual information, did not predict a forager's latency to leave the nest after its last interaction, regardless of whether we considered the proportion of interactions (Table 2) or the absolute number of interactions (Table 3, Fig. 3b). Similarly, the time at which a forager entered the nest, a proxy for colony satiation, did not affect a forager's latency to leave the nest after its last interaction. The random effect colony ID explained only 1% of the variance in the statistical model that considered the absolute

Table 1
Statistical output for the GLMM of a forager's time spent in the nest as a function of the proportion of interactions

Fixed effect	Estimate	SE	<i>t</i>	χ^2	<i>P</i>
Proportion of trophallaxis with fed	1791	238	7.52	56.47	<0.0001
Proportion of trophallaxis with hungry	1361	197	1.07	49.93	<0.0001
Proportion of mouth-to-mouth with fed	231	237	0.98	0.96	0.328
Proportion of mouth-to-mouth with hungry	240	317	0.76	0.58	0.447
Proportion of antennate with fed	199	171	1.17	1.36	0.243
Regurgitate	386	178	21.67	469.76	<0.0001
Time to enter nest	0.016	0.02	0.78	0.6	0.438

Interactions were included as proportions in this model, so the last interaction (proportion of antennate with hungry) could not be included in the model because it provided redundant information. Significant outcomes are shown in bold.

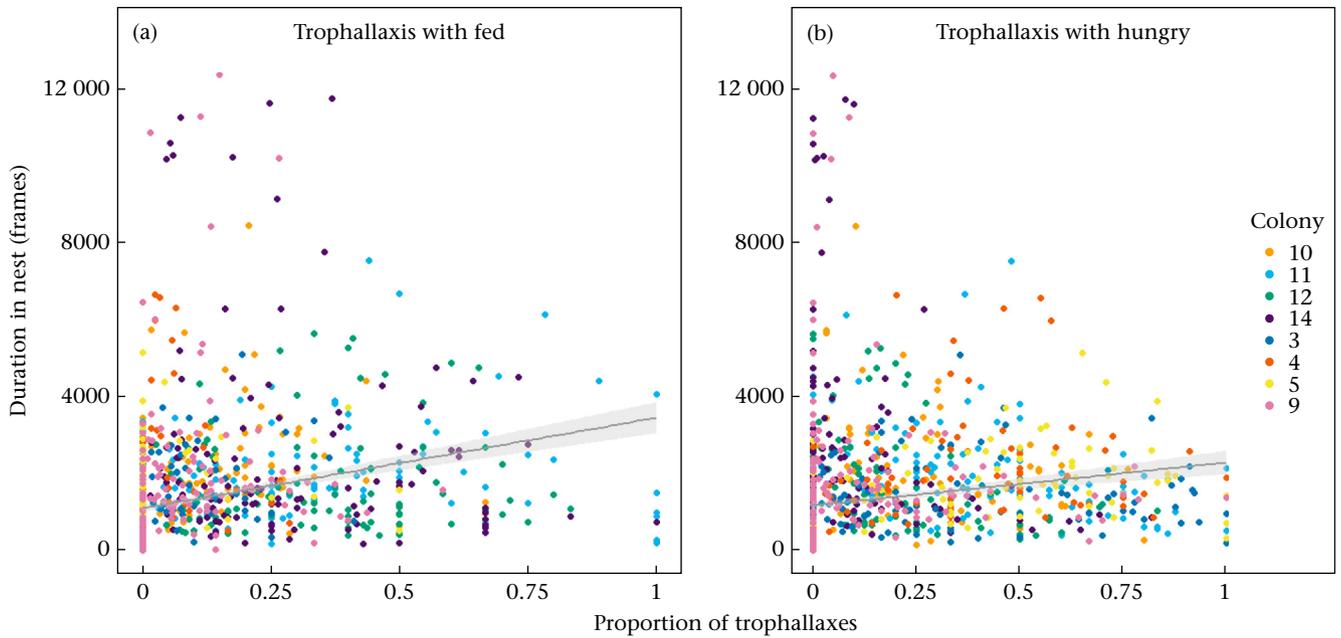


Figure 2. Predictors of time spent in the nest. The amount of time (in frames) a returning forager spent inside the nest before leaving it to continue foraging (duration in nest) as a function of the proportion of all interactions with (a) fed or (b) hungry ants when performing trophallaxis. Each point represents a single forager's visit to the nest and points are coloured by colony (see legend); grey lines show the relationship between the variables with a 95% confidence interval as a grey shadow using the GLM fit in 'ggplot2' (Wickham, 2016); solid lines depict statistically significant relationships.

number of interactions and 3% in the model that considered the proportion of interactions.

DISCUSSION

We found that a forager's decision to leave the nest and continue foraging depended on the type of interactions it experienced and who it encountered (fed or hungry ants) but not on its personal information or the colony's state. Interactions differed in the information they provided foragers about colony needs. As foragers spent more time in the nest, they had more interactions of all types;

however, only the proportion of trophallaxis interactions was positively related to the amount of time a forager spent in the nest. The latency to depart from the nest and continue foraging was related to the number of interactions a forager had with fed ants and the proportion of trophallaxis events they had with hungry ants, but not to the proportion of other types of interactions they experienced. Interestingly, neither personal information nor colony satiation predicted a forager's latency to leave the nest and continue foraging.

When examining the proportion of interactions of each type, only the proportion of trophallaxis interactions increased with the

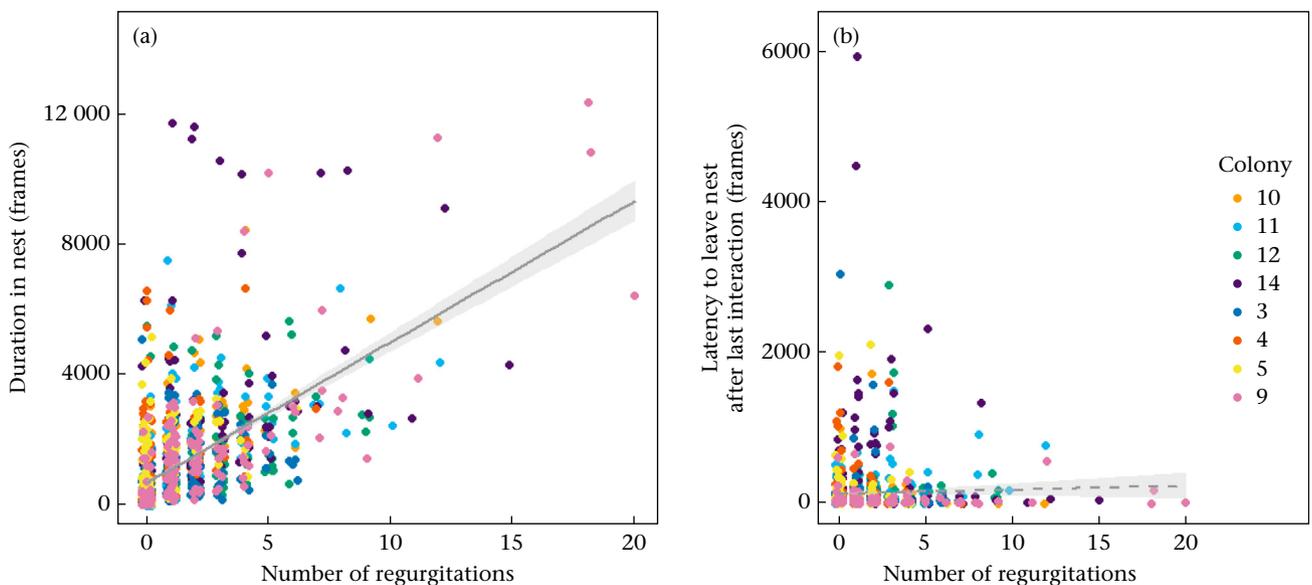


Figure 3. Effect of regurgitation (individual information) on forager decisions. (a) Total time spent in nest and (b) latency to leave the nest after the last interaction as a function of a forager's number of regurgitation events, i.e. the number of times a forager regurgitated food but no ant came to feed on it (individual information). Symbols, solid lines and shadow designations as in Fig. 2; dashed lines show nonsignificant relationships based on the GLMM described in the text.

Table 2

Statistical output for the GLMM of a forager's latency to leave the nest after its last interaction as a function of the proportion of interactions

Fixed effect	Estimate	SE	<i>t</i>	χ^2	<i>P</i>
Proportion of trophallaxis with fed	99.59	63.22	1.58	2.48	0.115
Proportion of trophallaxis with hungry	150.42	51.62	2.91	8.49	0.004
Proportion of mouth-to-mouth with fed	74.6	63.18	1.18	1.39	0.238
Proportion of mouth-to-mouth with hungry	21.52	84.98	0.25	0.06	0.8
Proportion of antennate with fed	−23.23	45.46	−0.51	0.26	0.61
Regurgitate	3.18	7.78	0.67	0.44	0.504
Time to enter nest	0.005	0.005	0.99	0.97	0.325

Interactions were included as proportions in this model, so the last interaction (proportion of antennate with hungry) could not be included in the model because it provided redundant information. Significant outcomes are shown in bold.

time a forager spent in the nest, even though, as one might expect, the more time a forager spent in the nest, the more interactions it experienced overall. This finding highlights the importance of examining trophallaxis interactions within the context of other interactions that a forager experiences. The foragers in our study were returning with liquid food in their crops that needed to be offloaded to other ants, through trophallaxis, before a forager could leave the nest to continue foraging, similar to other ants (Greenwald et al., 2015; Wallis, 1964). The time required to offload food depends on the space that receiving ants have in their crop to uptake food from foragers. Hungry ants have an empty crop, which allows them to receive more food from a forager compared to partly full crops of fed ants. It appears that the amount of time a returning forager spends in the nest is determined by the time it takes to offload its food through trophallaxis, similar to honey bees (Seeley, 1989). When a forager returns to a fed colony, it may experience many short trophallaxis interactions because each interaction will offload only a small amount of the food in its crop. This may explain the positive relationship between the time an ant spends in the nest and the proportion of trophallaxis interactions with fed ants, because the more fed ants there are, the more ants a forager needs to find to offload its food. When a forager returns to a hungry colony, it will empty its crop quickly via few trophallaxis interactions with hungry ants that each offload a large amount of food. Sometimes, when the colony is hungry, a forager may offload its food to multiple hungry ants simultaneously (Howard &

Tschinkel, 1980; Wallis, 1964; J. S. Miller & N. Pinter-Wollman, personal observations). Therefore, few trophallaxis interactions with hungry ants are required to quickly offload the foragers' food, explaining the positive relationship between the time a forager spends in the nest and the proportion of trophallaxis interactions it has with hungry ants. The explanation above assumes a well-mixed population in which a forager is equally likely to interact with any worker in the nest. Recent work suggests that how deep a forager moves into the nest might influence its decision to continue foraging (Baltiansky et al., 2023). Future work could examine whether the location of fed and hungry ants in the nest changes as the colony becomes satiated and affects forager interactions and decisions. Finally, we expect that the presence of larvae would change the impact of trophallaxis interactions with workers on forager decisions, because larvae are important recipients of liquid food and their food consumption is regulated by the rate of trophallaxis between foragers and larvae (Cassill & Tschinkel, 1996).

Regurgitation behaviour also corresponded to the amount of time a forager spent in the nest. We defined regurgitation as a forager bringing up food from its crop and holding it in its mandibles while not interacting, because nestmates were not nearby. By regurgitating, the forager is potentially anticipating a trophallaxis partner. Thus, if other ants do not approach to take the food (e.g. because they are not hungry), then a forager will have more instances of regurgitation and it will therefore stay in the nest for

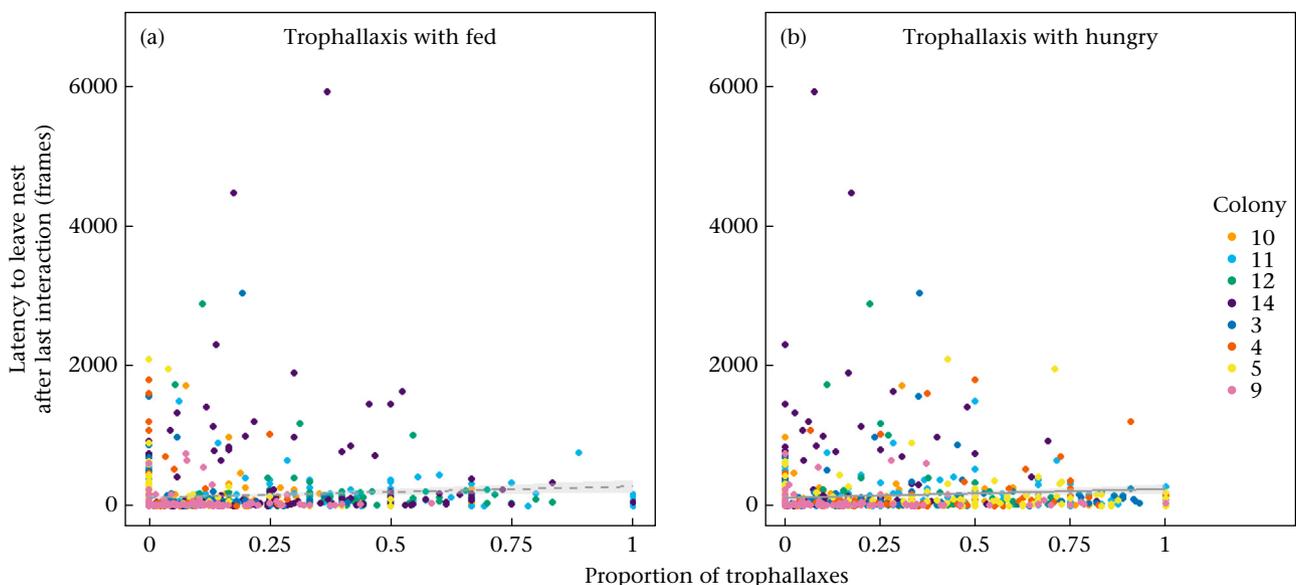


Figure 4. Predictors of a forager's latency to leave the nest after its last interaction. The number of frames a returning forager spent inside the nest from its last interaction with an ant until leaving the nest (latency to leave nest after the last interaction) as a function of the proportion of trophallaxis interactions with (a) fed or (b) hungry ants. Symbols, solid lines and shadow designations as in Fig. 2; dashed lines show nonsignificant relationships based on the GLMM described in the text.

Table 3

Statistical output for the GLMM of a forager's latency to leave the nest after its last interaction as a function of the absolute number of interactions

Fixed effect	Estimate	SE	t	χ^2	P
Trophallaxis with fed	10.84	2.98	3.63	13.16	0.0003
Trophallaxis with hungry	7.78	2.3	3.38	11.44	0.0007
Mouth-to-mouth with fed	31.48	4.81	6.54	42.73	<0.0001
Mouth-to-mouth with hungry	−5.88	6.43	−0.91	0.84	0.36
Antennate with fed	−3.91	0.92	−4.26	18.12	<0.0001
Antennate with hungry	−1.83	2.26	−0.82	0.67	0.41
Regurgitate	−2.8	5.23	−0.54	0.29	0.59
Time to enter nest	0.01	0.01	1.35	1.83	0.17

Significant outcomes are shown in bold.

longer, thereby reducing its foraging rate. These findings are similar to those of Seeley (1989), who found that honey bee foragers use the time they wait to offload their food to decide whether or not to continue foraging. Furthermore, our findings are consistent with those of Greenwald et al. (2018), who showed that a forager's decision to forage is based on the amount of food it has in its crop. However, the global state of the colony does not affect foraging decisions. In our study, the satiation of the colony was not a reliable predictor of the time a forager spent in the nest. One might expect that the hungrier the colony is (i.e. the earlier a forager returns to the nest), the shorter the forager visits will be, so it can continue to bring food to the colony. However, it appears that foragers do not have knowledge about the global state of the colony and the time they spend inside the nest is predominantly related to their local interactions rather than to the global state of the colony.

A forager's latency to leave the nest and continue foraging after its last interaction was best predicted by its interactions with fed ants and the proportion of trophallaxis interactions it had with hungry ants. The more interactions a returning forager had with fed ants, the longer it took to leave the nest. It is possible that a larger number of interactions with fed ants was an indicator that the colony was satiated, and foraging was not required, thus increasing the forager's latency to leave the nest. Future work might examine forager decisions when a colony is fully satiated, i.e. beyond the duration of our experiments that concluded once most ants in the colony were fed. For example, foragers in satiated colonies might stay in the nest and not leave it until food is consumed, or they might leave the nest without offloading all their food. Surprisingly, as the proportion of trophallaxis interactions with hungry ants increased, it took the forager longer to leave the nest. One might expect that as the proportion of forager's interactions with hungry ants increases, the forager will perceive greater colony hunger and leave the nest sooner to continue foraging and bring more food back to the nest. However, because liquid food takes time to transfer from the full forager to the hungry ants (Wallis, 1964), the greater the proportion of interactions a forager has with hungry ants, the longer it might take to offload the food and leave the nest from the onset of an interaction. Because we quantified a forager's latency to leave the nest as the time that elapsed from the start of its last interaction until leaving the nest, it is possible that, if a forager's last interaction was trophallaxis with a hungry ant (as it is likely to be if the proportion of trophallaxis events with hungry ants is high), then the time that the forager took to offload food led to longer trophallaxis interactions and therefore longer latencies to leave the nest, compared to other interactions, which were shorter. Interestingly, neither individual information (regurgitation), nor colony satiation predicted a forager's latency to leave the nest.

Our findings suggest that foragers rely predominantly on local and particular social interactions to obtain information about colony hunger level, rather than on personal or global information. Thus, social information, gained from a particular type of interactions,

trophallaxis, is more important than personal information for a forager when deciding whether or not to continue foraging. While past work on social insects and other biological systems (Sumpter, 2010) has uncovered the importance of local interactions for the emergence of collective outcomes, we highlight that not all interactions provide the same type of information. Some interaction types, like trophallaxis in this study, along with the state of the individuals one interacts with, like being hungry as found in this work, have a greater impact on decision making than other types of interactions, such as antennation or interactions with fed individuals. Thus, it is important to consider the nature of local interactions, and not only their rate or quantity, when studying emergent collective outcomes.

Author Contributions

J. S. Miller designed the study, collected and curated all the data. N. Pinter-Wollman analysed the data and wrote the first draft of the manuscript.

Data Availability

The raw data and analysis code for this study are available as supplementary material and on Zenodo (<https://zenodo.org/record/8132463>; Pinter-Wollman, 2023).

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2023.07.008>.

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Appendix

Table A1
Statistical output for the GLMM of a forager's time spent in the nest and the number of interactions

Fixed effect	Estimate	SE	T	χ^2	P
Number of trophallaxis with fed	159.4	7.35	21.68	470.03	<0.0001
Number of trophallaxis with hungry	97.21	5.69	17.09	292.02	<0.0001
Number of mouth-to-mouth with fed	161.33	11.86	13.6	184.99	<0.0001
Number of mouth-to-mouth with hungry	60.03	15.99	3.75	14.09	0.0002
Number of antennate with fed	12.65	2.27	5.58	31.16	<0.0001
Number of antennate with hungry	-1.15	5.5	-0.21	0.04	0.835
Regurgitate	200.6	12.71	15.78	249.07	<0.0001
Time to enter nest	0.07	0.01	5.98	35.75	<0.0001

Significant outcomes are shown in bold.

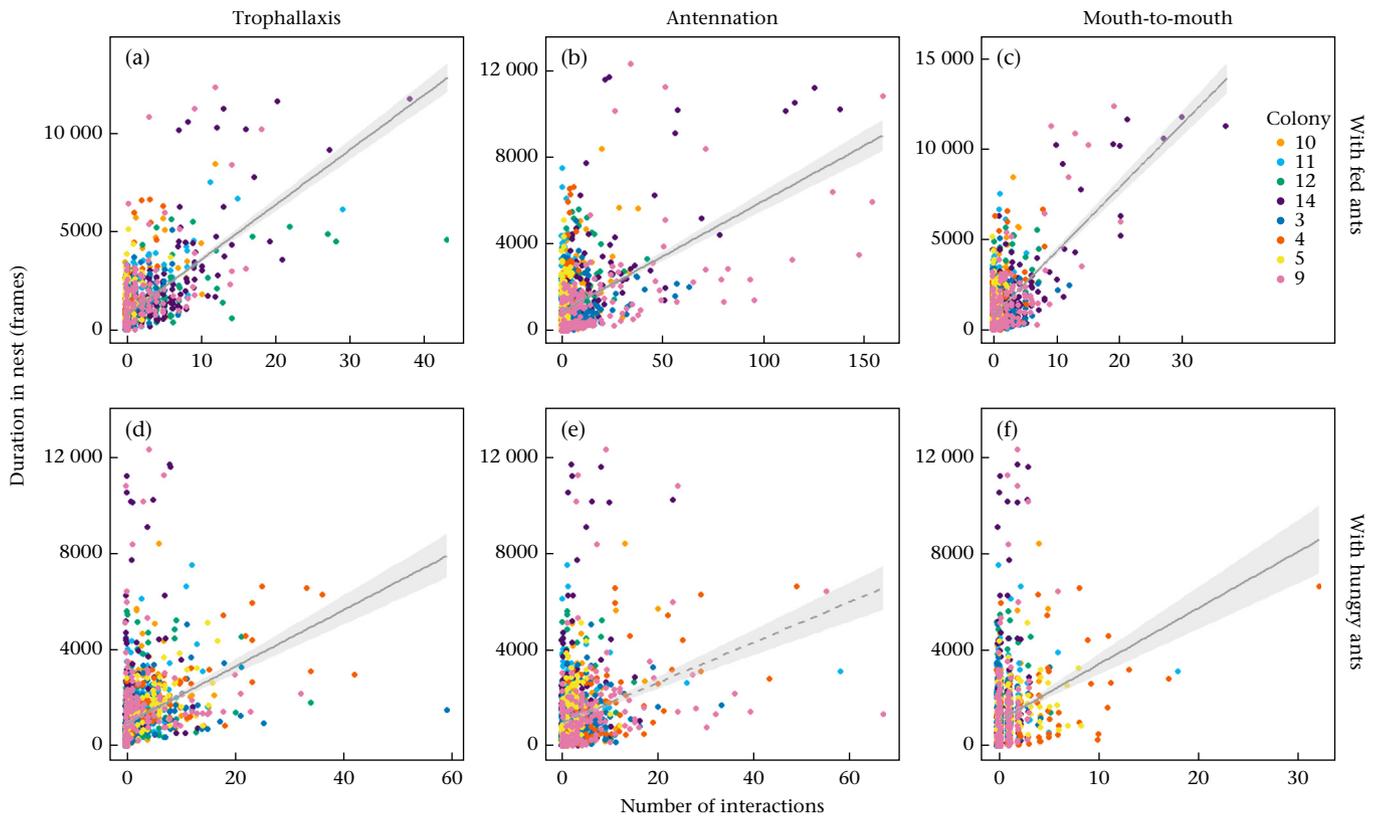


Figure A1. Predictors of time spent in the nest. The number of frames a returning forager spent inside the nest before leaving it to continue foraging (duration in nest) as a function of the number of interactions with (a–c) fed or (d–f) hungry ants when performing (a, d) trophallaxis, (b, e) antennation or (c, f) mouth-to-mouth interactions. Each point represents a single forager's visit to the nest and points are coloured by colony (see legend); grey lines show the relationship between the variables with a 95% confidence interval as a grey shadow using the GLM fit in 'ggplot2' (Wickham, 2016); solid lines depict statistically significant relationships; dashed lines show nonsignificant relationships based on the GLMM described in the text.

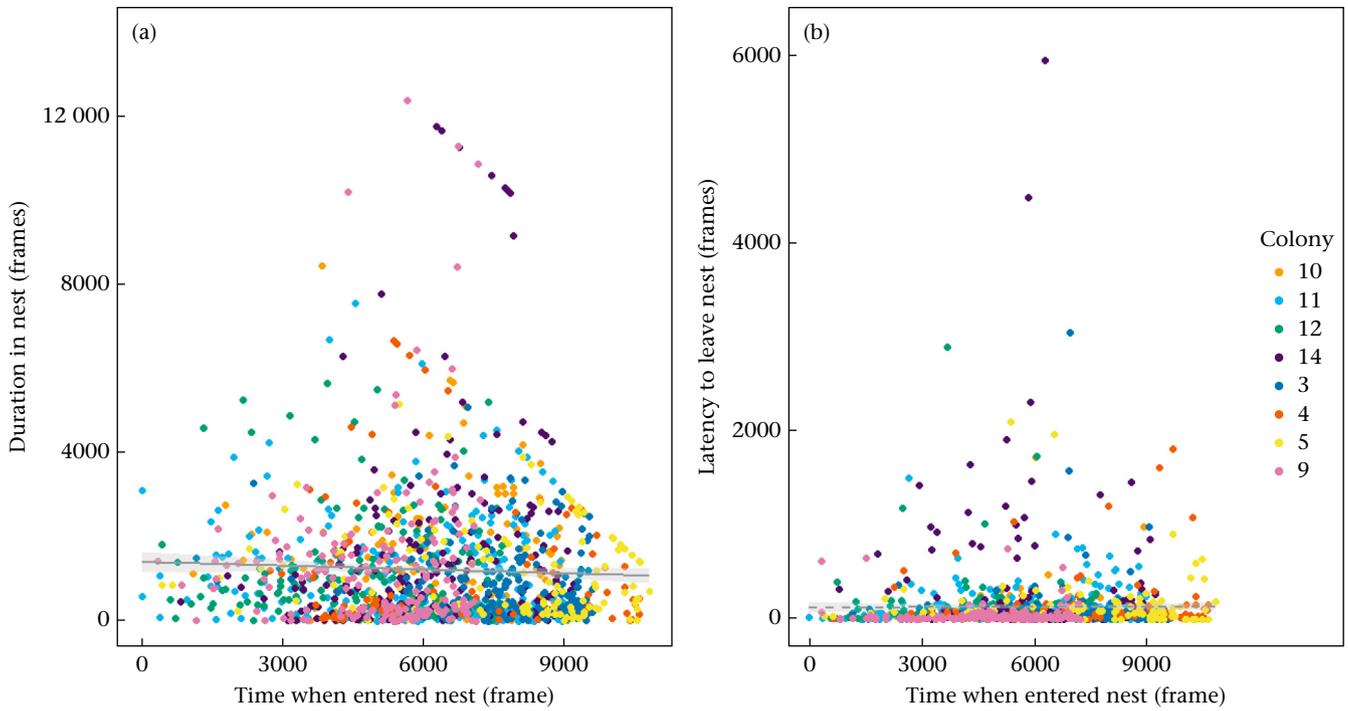


Figure A2. Effect of time to return to nest on forager decisions. (a) Total time spent in nest and (b) latency to leave the nest after the last interaction as a function of the time (frame) at which a forager returned to the nest, i.e. the satiation of the colony, which increased over time. Symbol, line and shadow designations as in Fig. A1.

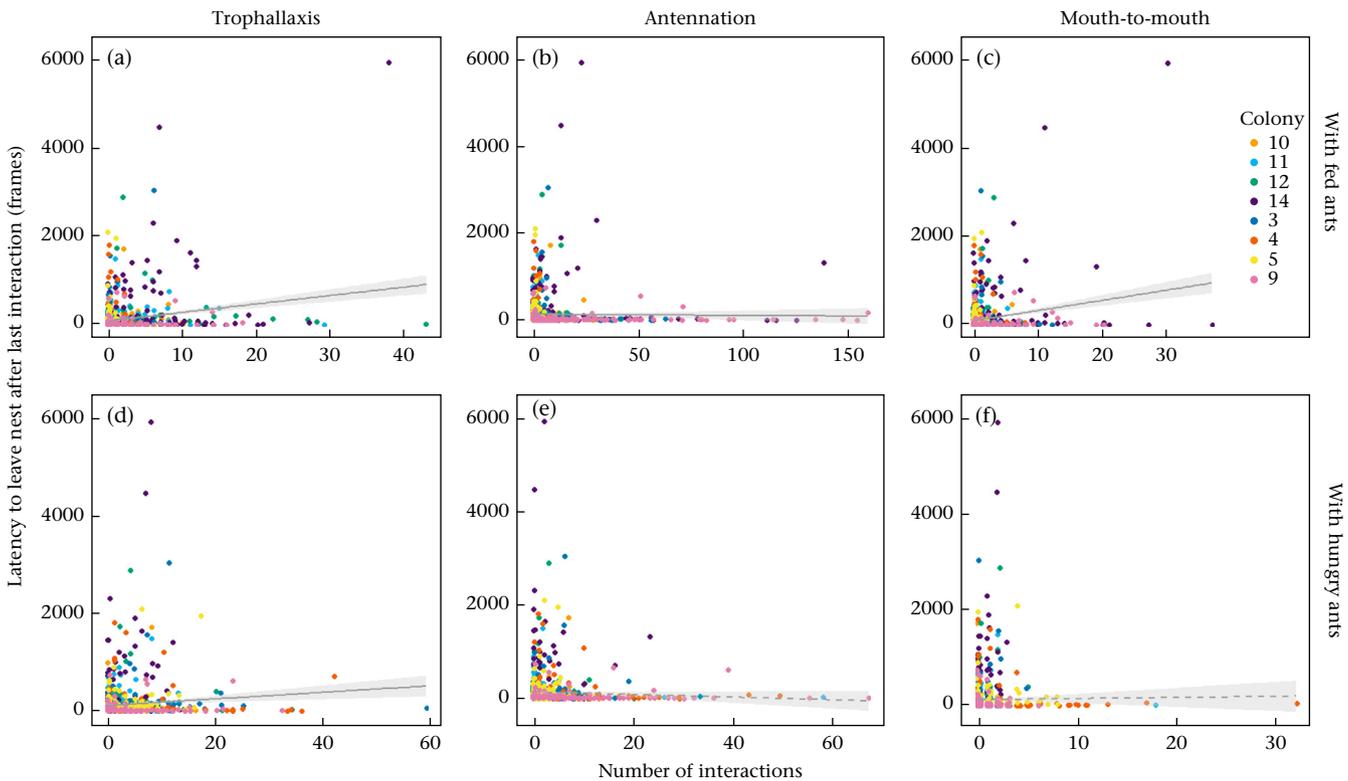


Figure A3. Predictors of latency to leave the nest after the last interaction. The number of frames a returning forager spent inside the nest from its last interaction with an ant until leaving the nest (latency to leave nest after the last interaction) as a function of the number of interactions with (a–c) fed or (d–f) hungry ants when performing (a, d) trophallaxis, (b, e) antennation or (c, f) mouth-to-mouth interactions. Symbol, line and shadow designations as in Fig. A1.