Report

Teaching with Evaluation in Ants

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Summary

Tandem running in ants is a form of recruitment in which a single well-informed worker guides a naive nestmate to a goal [1–8]. The ant *Temnothorax albipennis* recently satisfied a strict set of predefined criteria for teaching in nonhuman animals [9, 10]. These criteria do not include evaluation as a prerequisite for teaching [10]. However, some authors claim that true teaching is always evaluative, i.e., sensitive to the competence or quality of the pupil [11–13]. They then assume, on the premise that only humans are capable of making such necessarily complex cognitive evaluations, that teaching must be unique to humans. We conducted experiments to test whether evaluation occurs during tandem running, in which a knowledgeable ant physically guides a naive follower to a goal. In each experiment, we interrupted the tandem run by removing the tandem follower. The response of the leader was to stand still at the point where the tandem run was interrupted. We then measured how long the leader waited for the missing follower before giving up. Our results demonstrate *T. albipennis* performs three different kinds of evaluation. First, the longer the tandem has proceeded the longer the leader will wait for the follower to re-establish contact. Second, ant teachers modulate their giving-up time depending on the value of the goal. Finally, leaders have shorter giving-up times after unusually slow tandem runs.

Results and Discussion

Forms of teaching have recently been reported in one invertebrate, the ant *Temnothorax albipennis* [9] and two vertebrates, the Meerkat, *Suricata suricatta* [14], and the pied babbler, *Turdoides bicolor* [15]. These demonstrations employ a teaching definition that is well established in animal behavior, behavioral ecology, and evolutionary biology [10]. The above definition does not invoke evaluation or sensitivity during the teaching process, although such characteristics are thought to be of key importance for certain forms of teaching in humans. Indeed, some authors claim that true evaluative teaching is unique to humans, involving theory of mind based intentionality or cultural transmission [11–13, 16, 17].

In behavioral ecology, however, evaluation has been shown in many different contexts to be based on relatively simple rules of thumb. For example, female cockroaches use internal thresholds to select among potential mates [18], and an optimal forager should leave a patch when its instantaneous rate of gain falls to the overall rate for the environment as a whole [19, 20]. Neither of these are claimed to require higher mental states even when the assessor is sensitive to signals from other individuals rather than environmental cues.

Certain authors have assumed that animal teaching, if it occurred at all, would be quite circumscribed because it would be limited solely to foraging, without sensitivity to progress [11–13]. However, unlike other recently described cases of animal teaching [14, 15], tandem running is not so restricted, occurring not only for foraging but also in three other specific contexts: in colony emigration, in exploration of newly discovered territory [21, 22], and also for the transmission from leader to follower of spatial fidelity to specific foraging areas [23]. During tandem recruitment, one worker directly leads a nestmate to a goal. Contact is maintained between the pair by the follower tapping the leader's gaster and hindlegs with her antennae [3, 5–8].

During colony emigration, our focus in this study, nest-site scouts only initiate tandem recruitment in the early stages of information dissemination, before a quorum is achieved at the new nest. After the quorum is achieved, they switch to nest-mate carrying, which is three times faster than tandem running [24]. The quorum threshold, and hence the decisions to switch from tandem running to social carrying, is attuned to several factors including colony size and a tradeoff between speed and accuracy. When harsh conditions favor speed of decision making over the sharing of information, fast carrying predominates. When time is less pressing, information dissemination is more frequent through slow tandem running [25].

Tandem running can operate both to and from a target [4], although reverse tandem runs only occur during nest emigration (T.O.R. and N.R.F., unpublished data). Here, we will call "forward" tandem runs those that lead from the old nest to a new one; "reverse" tandem runs lead in the opposite direction. Such tandem followers often become recruiters, i.e., tandem leaders [4]. In either case, the leader frequently waits for contact from the follower, and only when such physical contact recommences does the tandem leader continue [2, 3, 8, 9]. Only after a considerable time will a leader give up and move away if contact is not made (in some cases a leader waited for over 1 min during a tandem that would normally take

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2–3 min to complete [T.O.R. and P.A.S., unpublished data]). We used this giving-up-time (GUT) as a metric to determine whether leaders evaluate (1) their investment in the tandem, (2) the value of the tandem in terms of the quality of the goal, and (3) the behavior of the follower and/or the speed of the tandem run. Our basic method was to remove the follower and determine how long the leader was prepared to wait before giving up on the follower.

Costs and Benefits

To determine the optimal GUT for the leader, we developed a model in which we consider a leader that has lost contact with the follower at some point on its path. Let T denote the average time it would take the leader to return to the current position with a follower. This might involve several trips to the nest to find a new follower that remains in contact up until this point. Assume that the leader has waited for a time t without re-establishing contact. We compare the consequences of giving up immediately with the consequences of waiting for a further time δ and then giving up if the follower has not reconnected (here, δ is assumed to be small). If the leader gives up immediately, then the average time to return to the current position with a follower is T. If the leader waits, the average time is

$$\delta + (1 - p(t, \delta))T$$

where $p(t, \delta)$ is the probability of reconnection in the time interval of length δ. Thus, it is best to give up immediately if

$$p(t, \delta)T \leq \delta.$$

For small δ, $p(t, \delta)$ is approximately proportional to δ so that we can write $p(t, \delta) = h(t)\delta$, where the constant of proportionality $h(t)$ depends on the elapsed time t. The function $h(t)$ is the familiar hazard function of reliability theory. From this we see that it is best to give up immediately if

$$h(t) \leq \frac{1}{T}.$$

In other words, $h(t)$ acts as a marginal rate. When this falls to the "overall" rate $1/T$, it is optimal to give up. At least for a large t, $h(t)$ will decrease, i.e., the reconnection rate decreases as the time since the connection was lost increases. Therefore, the greater the time T is required to regain the current position with a follower, the longer a leader should wait. Because T will tend to increase with either the distance from the nest at which contact is lost or the duration of the run, it is optimal to wait longer as this aspect of investment increases.

Because in the model, T increases with past investment, GUT should increase with past investment. We thus tested the null hypothesis that GUT is insensitive to time invested. This was done by systematically interrupting forward tandem runs (removing the follower) so that we could determine how long the leader would wait as a function of her investment so far. We found that the greater the duration of the tandem, the longer the tandem leader waits for missing followers (Figure 1). Therefore, leaders risk more time being potentially wasted as
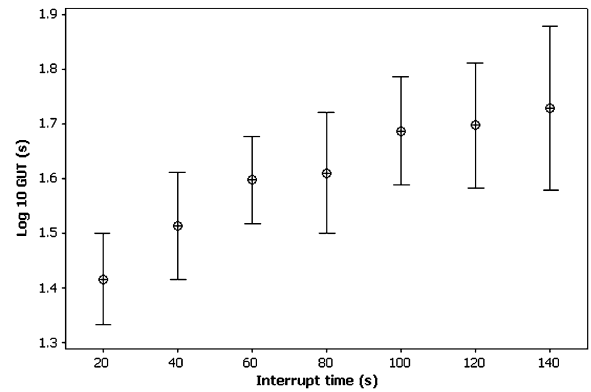

Figure 1. Leader Giving-Up Times Vary According to the Length of Time the Tandem Has Proceeded

$\log_{10}$-transformed GUT for seven interrupt times ($n_{20} = 37$, $n_{40} = 29$, $n_{60} = 30$, $n_{80} = 32$, $n_{100} = 23$, $n_{120} = 22$, and $n_{140} = 12$). Error bars represent 95% confidence intervals for the means. Weighted least-squares fit: $r^2 = 0.14$, $\log_{10}$ GUT = $0.36*\log_{10}$ interrupt + 0.943, F = 29.9, *d.f. = 1,183*, p < 0.0001.

a function of time invested. However, such behavior is not necessarily an example of the so called "Concorde fallacy" [26, 27] with increasingly irrational investment chasing earlier wastefulness. If future consequences depend on past costs, then those costs should be taken into account [28, 29]. In the case of tandem runs, during which the leader continues to the target alone if the follower fails, we have shown that it is optimal for waiting time to increase as past investment (represented by T) increases.

The above model assumes that the leader uses time as the metric for its decision; however, there are alternatives such as distance traveled [30]. It is often difficult to discriminate between these alternatives. Indeed, the cue the leader might use to assess progress toward the goal and adjust her GUT accordingly could be a distance-related proxy, for example the density of home-range marking, as in mass-recruiting ants [31]. Crucially though, these metrics all positively correlate with one another.

Other social insects intensify their communication as they approach a foraging site [31, 32], so the longer giving-up times of tandem leaders as they approach the new nest site may also be regarded as such a graded recruitment effort.

Here, we have shown sensitivity to progress in tandem running in *T. albipennis*. This implies an assessment of progress that correlates with past investment and a concomitant adjustment in current investment. Evaluation of some form is clearly occurring in such tandem running.

Value of the Goal

Next, we compared GUT in both forward and reverse tandem runs to and from good and poor new nest sites. Clearly, leaders will wait longer for followers during forward tandem runs to good nests rather than to poor ones but the opposite is the case for reverse tandem runs (Figure 2). This behavior could be considered functionally analogous to mass-communicating ant species modulating trail-laying intensity as a function of food-source quality [33]. Earlier work showed that these
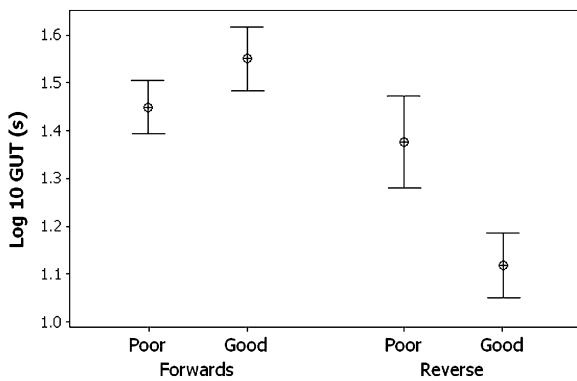
Figure 2. Leader Giving-Up Times Vary According to the Direction of the Tandem and the Value of the Goal

GUT by tandem direction and target quality (forward, poor—n = 116; forward, good—n = 88; reverse, poor—n = 41; reverse, good—n = 73). Error bars represent 95% confidence intervals for the means. Forward tandem runs—good quality verses poor: Student's t test on $\log_{10}$-transformed GUT, p = 0.021, T = 2.33, d.f. = 182. Reverse tandem runs—good quality verses poor: p < 0.0001, T = 4.40, d.f. = 79. The "finishing line" was closer to the old inner nest than the outer target nests, so forward and reverse abandon times were not compared statistically.

ants are able to use multiple metrics to differentiate between good- and poor-quality nests [34] and that they encode nest quality by hesitating less before recruiting by tandem running to good nests [35]. Their greater hesitation over poor nests creates a time lag and may help the ants to find better nests. Hence, it is possible that forward tandem leaders, when they rapidly abandon followers on the way to poor nests, are contributing to useful delays. The longer the GUT they exhibit when leading forward tandem runs to a high-quality nest could, by contrast, help them quickly to build a quorum for a valuable goal. Reverse tandem leaders returning from poor nests may wait longer for lost followers because poor nests are likely to have received fewer forward tandem runs [24, 35]. Hence, once an individual decides upon such a nest, there may be a pressing need to compensate by carefully showing more ants an efficient route to that nest.

Speed of the Tandem Run

Finally, we tested for direct evaluation by leaders of the performance of quick and slow tandems. To do this, we created a class of poor tandems by amputating one of the follower's antennae [36]. Tandem runs with followers with one antenna are much slower than those with two (Figure 3). We considered only the speed difference between tandems with followers with two antennae versus those with one, irrespective of the leader's number of antennae, because leader antennae number had no significant effect on the GUT (Figure 4, legend). Tandem leaders appear to adjust their GUT in relation to the rate of progress of the tandem (Figure 4).

Although we tested for an effect of nest quality and tandem direction, there was no a priori reason for predicting the direction of the effects. Therefore, we did not expect leaders to display a greater or lesser GUT when participating in a slower tandem. Leaders, however, displayed significantly longer GUT during fast tandems
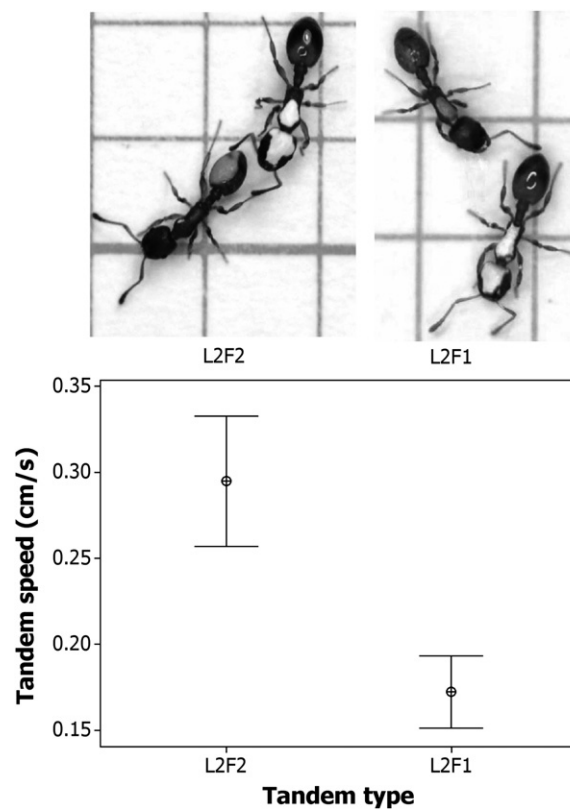

Figure 3. Comparison of Overall Speed of Tandem Pairs

L2F2 represents both leaders and followers with two antennae; n = 20, mean 0.29 cm/s. L2F1 represents leaders with two antennae and followers with one; n = 20, mean 0.17 cm/s. Error bars represent 95% confidence intervals for the means. Student's t test; p < 0.0001, T = 5.92, and d.f. = 29.

compared to slow ones (Figure 4) and thus did not invest extra time when participating in less effective tandem runs but rather selectively discriminate against such occurrences. One possible reason for leaders having longer giving-up times after faster tandem runs is that once contact has been re-established, they might proceed to the goal in a shorter time.

We cannot yet be sure of the proximate causal chain linking antennal amputation to slow tandem speed. Given the normal bidirectional feedback between tandem leader and follower [9], the slowness might result from the behavior of the follower, the leader, or both, although we do not consider these explanations to be mutually exclusive. It is unlikely that manipulated followers are slow learners per se because current evidence suggests that navigating ants of the genus *Temnothorax* (*Leptothorax*) employ visual cues more than pheromone trails [21, 37, 38]. Therefore, we tentatively suggest that tandem runs with manipulated followers are slow because the coupling between the follower and the leader is perturbed. In turn this might be because, with only one antenna, the follower struggles to assess accurately the leader's body orientation and hence the direction of travel. Alternatively, as a result of infrequent or asymmetric antennal contacts, the leader might move for a shorter distance or for a shorter length of time after each bout of antennal contact. It is
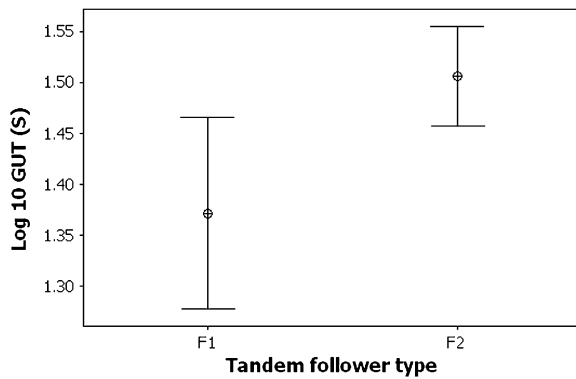
Figure 4. Log 10 GUT by Follower Antennal Number

(L2F1, n = 36; L1F1, n = 8; L2F2, n = 170; L1F2, n = 21). Error bars represent 95% confidence intervals for the means. Leader antenna number: L1 versus L2; Student's t test on $\log_{10}$-transformed GUT, p = 0.064, T = 1.91, and d.f. = 41. Follower antenna number: F1 versus F2; p = 0.013, T = 2.54, and d.f. = 69. A GLM including the interaction of leader antenna number with follower antenna number demonstrated this factor combination to be not significant (p = 0.25, F = 1.3, and d.f. = 1).

also possible that the shorter giving-up times of ants leading manipulated followers are simply a direct consequence of such limited or asymmetric stimulation and has no ultimate relevance. However, we simply note that tandem runs with amputated followers do occur naturally, so the likelihood of the variable GUT being merely artifactual is perhaps diminished. To investigate this further, we will try to determine in future work the mechanisms behind slower tandem runs and shorter giving-up times.

Conclusions

Evaluative teaching should have the advantage of reducing costs that might otherwise be incurred by uncontrolled investment under unproductive circumstances. Social insect colonies are characterized by regulatory-feedback loops [39], so the evaluative teaching we have demonstrated might be usefully regarded as a loop that regulates investment by the leader.

By contrast, meerkat teaching appears not to involve direct evaluation of the abilities of the pupil by the teacher. Playback experiments show that teachers modify the learning opportunity they provide according to the age-related calls of pups rather than their actual prey-handling skills [14]. By contrast, our experiment 3 suggests that the actual performance of the follower during the tandem might directly influence the behavior of the leader.

Leadbeater et al. [40], in reviewing Franks and Richardson [8], lumped both tandem running and the honeybee waggle dance together as forms of "telling." In their view locational information, by its very nature, cannot be taught but must instead be told. Waggle dances, as they rightly pointed out, are used by one bee to "tell," i.e., inform, others about the distance, direction, and quality of food that they have discovered. The waggle-dance is a form of symbolic communication [41] that explicitly references an external cue (the sun). "Telling," by definition, occurs when one individual provides knowledge or informs another of a fact, for example, "go

North to find food." By contrast, in the ants, the leader actually shows another ant how to get from the nest to the goal. In this case, communication does not convey abstract or explicit symbolic reference to external stimuli. Rather, the leader and follower directly engage in the task and the actions and behaviors of the tandem-running procedure are directly coupled, in both time and space, to the information transmission itself. Consequently, we would contend that the tandem "teaching" procedure is a fundamentally different, although not necessarily more "advanced," mode of information transfer to referential "telling."

The lumping together of tandem running and waggle dancing by Leadbeater et al. [40] is potentially misleading because it detracts from the importance of the feedback that occurs in both directions between the leader and the follower in tandem running [8]. "Feedback" is typically defined as some coupling of output back to input. During tandem running, a bidirectional-feedback loop is clearly observed in the mutual and dynamic signal interchange; in response to the nature of the follower's tactile contact signaling (input), both leaders and followers antagonistically vary their acceleration (output), and this variation changes the nature of the input, and so on. Indeed, it is such feedback that might provide tandem leaders with some of the information they use for evaluative teaching. Conversely, in the waggle dance, although there certainly is occasionally one-way communication of flower quality from the dancer to attendees via trophallaxis (one in ten dance followers engage in trophallaxis), there is no evidence to show that information passes from the trophallactic recipient to the donor (T.D. Seeley, personal communication). Because there is no evidence for Markl's [42] "backward transmission" or "response monitoring" between waggle dancer and follower(s), we conclude that, at present, there is no evidence that the communication of locational information via the waggle dance requires bidirectional feedback. Indeed, trophallaxis is not an essential prerequisite for successful recruitment [43], and a waggle dancer may even dance when there are no bees in attendance (T.D. Seeley, personal communication).

The longstanding issue of whether the transmission of knowledge, as opposed to skills, qualifies as teaching [9] continues to be controversial [14, 15, 40]. Furthermore, whether a theory of mind should be a prerequisite for teaching is still being debated [11, 12, 44]. Three-year-old children can teach—or be taught—by direct demonstration [5]. However false-belief experiments suggest that they have not yet developed a complete theory of mind and are hence incapable of facultative perspective taking [45]. For example, three year olds do not appreciate that the teacher's belief about the pupil's knowledge determines whether the teacher will teach [13]. If human teachers can impart simple declarative knowledge without a theory of mind, then we would reason that such criteria should not be included in a minimum definition of teaching.

In this vein, we note that pleas for changes in the definition of teaching seem to be tracking our own understanding of what is special when humans teach, i.e., what it is to be a human pedagogue. We depart from Csibra [16] in that we consider it unproductive to

continually refine the criteria that define a behavior such as teaching in order that the definition more accurately reflect only the unique features of functionally similar, yet considerably more complex, "higher-order" behaviors in humans. By focusing on the underlying similarities among different taxa that achieve functionally similar outcomes, we would gain a deeper understanding both of the minimal criteria and the effects of the presence of more complex augmenting features. We should thereby avoid succumbing to the understandable temptation to use the most exotic, extreme case, i.e., the human one, to define what is perhaps a relatively common phenomenon.

Our findings suggest that simple forms of evaluative teaching might be based on thresholds and simple rules of thumb. This is not to deny the importance of other more sophisticated forms; rather, it adds to a deeper understanding of the richness and variety of communication systems that nonhuman animals exhibit.

Experimental Procedures

All ant colonies were collected in June 2006 from Dorset, UK. Experiments ran daily from 15/6/6 to 6/9/06 between the times 8:30 and 17:30. Colonies were fed ad libitum with dilute honey solution, *Drosophila*, and water.

A four-quadrant arena design was used so that nest-site comparisons could be minimized (Figure 5). The four outer Petri dishes were connected to the inner dish by acetate bridges upon which the grid lines were photocopied. The entrances to the outer nests were centered on the vertical and horizontal axes. The back wall of each nest was always placed 5 mm from the wall of the outer Petri dishes, whereas the orientation of the old (inner) nest was randomized for every trial.

Graph paper was fixed underneath the clear Petri dishes so that the observers could determine distances moved by the ants. When a tandem was interrupted, the follower was carefully removed, with a small brush, without touching the leader. We then observed the former leader and recorded the time that elapsed before she gave up and left. Leaders were deemed to have abandoned their follower when they moved more than 1.3 cm in any direction from their interrupt location. Once the leader had abandoned her follower, she was removed from the arena and isolated from the rest of the colony for the remainder of the emigration; only then was she repatriated. If any run was unobserved in error, then the leader was still isolated but no data recorded.

The old nest containing the ants was always placed in the center at the point marked X in Figure 5. To induce each colony to begin emigration, we removed the roof of the old nest. For all experiments, colonies were reused (mean emigrations/colony = 4.0, SEM = 0.28), although learning effects can be discounted because colonies were always left for the minimum 6 day "forgetting time" between emigrations [46]. In experiment 1, the number of emigrations had no effect of upon GUT (ANOVA on log 10 GUT, d.f. = 2,182, F = 0.81, and p = 0.45). For the forward tandem runs of experiment 2, there was no effect of experience among colonies that had accomplished different numbers of emigrations (ANOVA on log 10 GUT, d.f. = 2,200, F = 2.28, and p = 0.11). Because there were no appropriate comparisons, we did not test for an experience effect on reverse tandem runs in experiment 2 (all colonies were equally experienced) or when portions of colonies had had antennae removed in experiment 3.

Experiment 1. Costs and Benefits
We emigrated each of 18 colonies twice. They were given the choice of four equal, good-quality target nests (The cavities of the nests were 49 × 34 × 2 mm, with a 2.5-mm-wide entrance. The cavity was made dark with a red filter.). The colony was observed from the start of the emigration (time zero) when the roof of the old nest was removed. Each tandem run was observed from when it began at the old nest and was interrupted after it had proceeded toward
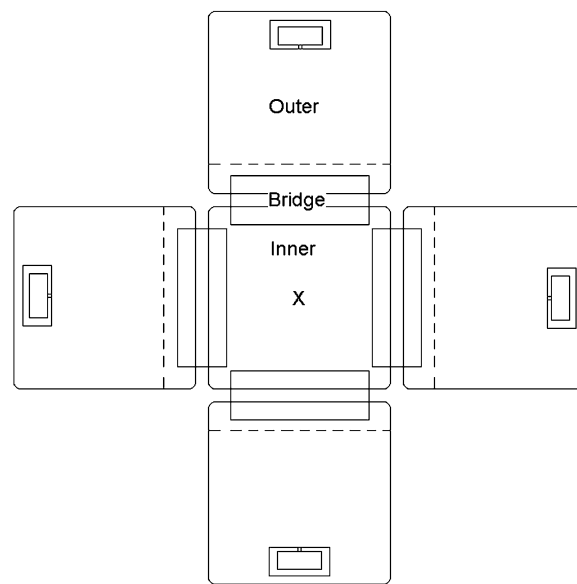

Figure 5. Plan View of Arena Layout

Each square Petri dish (23 × 23 cm) contained one microscope-slide nest at its outer edge. The old nest was placed in the central Petri dish at the (X). The dashed lines indicate the "finishing lines" at which tandem runs were interrupted in experiments 2 and 3; these lines were 1.3 cm from the end of the bridges.

the goal for a randomly chosen preset time period (20–140 s). We also recorded the time that each tandem started, relative to time zero, when the old nest was destroyed (GLM on time because the emigration started against Log 10 GUT, F = 1.63, and p = 0.20).

Experiment 2. Value of the Goal
Part A
Twenty five colonies were emigrated with a choice of one good-quality nest (49 × 34 × 2 mm, entrance 1.3 mm, and dark), and three poor-quality target nests (49 × 34 × 1 mm, entrance 4 mm, and light). During the emigration, all forward tandem runs were interrupted at the finishing lines. We recorded the time since the start of the emigration and the GUT. The target nest (N, E, S, and W), the time since the start of the emigration that the tandem passed the finishing line, and the quality of the nest (G and B) were recorded.
Part B
A similar interruption was conducted but for reverse tandems returning from any of the four target nests. Nineteen colonies were emigrated with three low-quality and one good-quality target nest. The forward tandem runs were not interrupted, but the time that they passed the line and the direction they were traveling were recorded. However, all of the reverse tandem runs were interrupted at the same "finishing" lines as the previous forward tandems.

Experiment 3. Speed of the Tandem Run
For creating a class of potentially poor followers, approximately one-third of the workers in certain colonies had one of their antennae amputated. Left or right antennae were chosen at random.

The nest was placed in a large Petri dish, and the roof was removed. The colony was then left to explore the dish for 5 min, and a perimeter of 1 cm was drawn around the outside of the nest. For the next 10 min, all the ants that were outside the perimeter were removed and placed into a separate holding dish. Half of the ants then remaining within the perimeter were selected for amputation with the more active ants being preferentially selected and added to the outside perimeter group. These subjects were temporarily anaesthetized with CO_2 gas. We then removed an antenna from each of the ants in the "outside 1 cm" group.

To determine whether the ants with only one antenna were indeed lower-quality followers, we induced five colonies into a further emigration that was filmed. Videos were digitized, and tandem

movements were analyzed with in-house tracking software. Tandems in which the follower had only one antenna and the leader had both were compared to an equal number of normal tandems.

Finally, for determining whether there was any difference in GUT between tandem pairs with different antennal combinations, workers that had received antennal amputations were left for at least 6 days before being emigrated. When the 23 colonies were emigrated, they had the choice of four good-quality target nests. During the emigration, all forward tandem runs that reached the "finish" line were interrupted, and the abandon time of the leader was recorded in the same way as the previous experiments. The antennal complement of both leader and follower, the time since the start of the emigration that the run passed the "finish" line, and the direction the run was heading were all recorded.

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