

# 20 Tandem Running Recruitment by *Temnothorax* Ants as a Model System for Social Learning

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Humans often use information from others to avoid the costs of personal exploration. For example, one of the authors (TS) recently moved to a new town in Georgia, United States of America, and tried to find good places to eat. Instead of going to random restaurants and trying them for himself, he asked his colleagues for recommendations. In this way, he was able to find good restaurants without spending most of his first precious salary on food. Many nonhuman animals also use information from others, known as social learning (Heyes, 1994; Laland, 2004; Hoppitt & Laland, 2013; Kendal et al., 2018). For example, if chimpanzees are presented a box of juice with a small hole and a straw, they typically try various inefficient methods, such as dipping the straw into the juice and licking it. As soon as one chimpanzee in the same group uses the straw “correctly” (i.e., sucking up the juice), others also adopt the more efficient method (Yamamoto, Humle, & Tanaka, 2013). Likewise, when red-winged blackbirds observe that conspecifics become ill after eating certain food, they avoid the food and the consequent illness without having to experience it (Mason & Reidinger, 1982).

Social learning has become a major focus of interdisciplinary research (Kendal et al., 2018), but there remain important areas that are little explored. For example, although studies have repeatedly shown that animals use social information in natural group settings (see Lefebvre & Aplin, 2017 for a review), we still know little about how they do so. This is partly because it is often hard to observe the information-transfer process when multiple individuals are present (Hoppitt & Laland, 2013). Imagine that some group members display a certain behavior, and another group member shows the same behavior moments after. Does this mean that s/he socially learned the behavior from these group members? Is it possible that s/he imitated only one of them, and if so, which one? Another possibility is that s/he learned nothing from the others but independently “innovated” the same behavior: Because it is often hard to directly observe social transmission among group members, researchers use statistical techniques to infer this process by

measuring information diffusion rates at the group level (Hoppitt & Laland, 2013; Kendal et al., 2018). In short, the social learning strategies (i.e., “when” and “who” to copy) (Laland, 2004) are often hard to observe in a natural group setting.

Furthermore, the field of social learning has overlooked or simplified emergent processes of collective performance. It typically assumes that groups improve their performance because one or a few group members gain useful new knowledge or innovate superior behaviors, and other members simply copy the innovators through social learning (Boyd & Richerson, 1988; Henrich, 2004). However, emergent processes of collective performance can be more complex. For example, small human groups can sometimes solve more cognitive tasks than the best member in the group working alone (Kerr & Tindale, 2004; Laughlin, 2011; Larson, Jr., 2013). This result cannot be explained by inferior group members simply imitating the “smartest” individual. Instead, the sharing of information seems to synergistically improve collective performance (Larson, Jr., 2013). This phenomenon, known as collective intelligence (Krause & Ruxton, 2002; Surowiecki, 2005; Krause, Ruxton, & Krause, 2010; Sumpter, 2010; Jayles et al., 2017), has rarely been studied in terms of social learning. The synthesis of these two fields can shed light on how feedback from learning may improve collective intelligence over time (Biro, Sasaki, & Portugal, 2016).

Our goal in this article is to show that tandem running recruitment by ants (see below for details) offers a promising model to study the interaction of social learning and collective intelligence. Although vertebrates have received more attention, social learning is also well known in the eusocial insects, such as ants, bees, and termites (Leadbeater & Chittka, 2007). These insects use a wide variety of signaling mechanisms to share information about the locations of valuable resources. A classic example is the honeybee waggle dance, by which successful scouts inform naïve nestmates of the direction and distance to food, water sources, or potential nest sites (von Frisch, 1967; Seeley, 1995). Recruits can in turn share this information with others, creating extensive communication networks that allow the colony to adaptively allocate foragers across competing food sources or choose the best new home among several options (Seeley, 1995, 2010). Other examples have been extensively reviewed elsewhere (e.g., Leadbeater & Chittka, 2007; Leadbeater & Chittka, 2009; Grüter, Leadbeater, & Ratnieks, 2010; Grüter & Leadbeater, 2014; Leadbeater & Dawson, 2017). Here we focus on the particular case of tandem running, a recruitment method used by some ant species, including those in the genus *Temnothorax* (Franks & Richardson, 2006; Franklin, 2014). We first review the role of tandem runs in the ecology and collective behavior of these ants. We then propose new investigations into how social learning via tandem runs affects their collective performance.

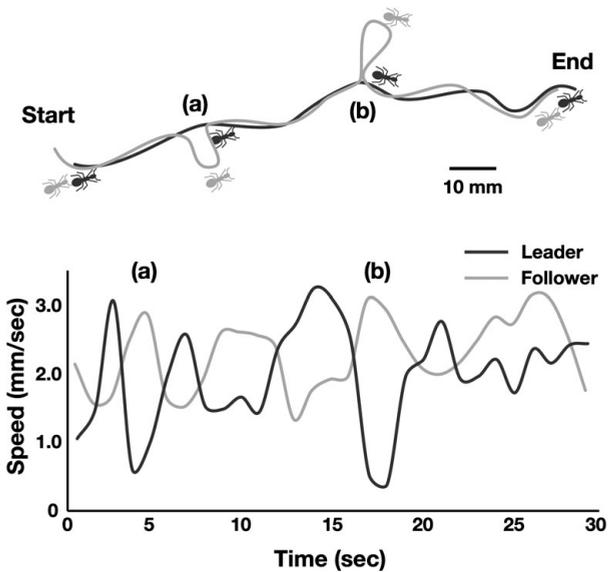
## What Is Tandem Running?

Tandem running was first recorded over 100 years ago by a Swedish researcher (Aldlerz, 1896; see details in Stuart, 1986), but it was not thoroughly described and analyzed until the 1970s (Möglich, Maschwitz, & Hölldobler, 1974). Although tandem running has been recorded in many species within at least three subfamilies (*Mymicinae*, *Formicinae*, and *Ponerinae*) (Franklin, 2014), here we focus on the myrmicine genus *Temnothorax* (formally *Leptothorax*), as their recruitment is very well studied, especially in the context of colony emigration and nest-site selection. Their small colonies, (usually 100–250 workers) typically live in rock crevices, twigs, or hollow nuts. Because these nest sites are short-lived, colonies must frequently emigrate to new homes (Möglich, 1978; Partridge, Partridge, & Franks, 1997). During these migrations, tandem runs play an important role in allowing scout ants that discover candidate nests to share this information with their nestmates (Pratt, Mallon, Sumpter, & Franks, 2002). *Temnothorax* foragers similarly use tandem runs to alert nestmates to the location of rich food sources (Franks & Richardson, 2006; Shaffer, Sasaki, & Pratt, 2013).

Whether the recruitment target is food or a nest site, tandem runs follow the same basic pattern. The successful scout or forager returns to her colony and releases a pheromone from her poison gland to attract a nest mate, whom she then slowly leads to the target (Möglich et al., 1974) (Figure 20.1). As they move, the follower regularly taps the leader's abdomen and hind legs with her antennae. Their progress is frequently interrupted by brief pauses in which the follower breaks contact with the leader and makes looping or searching motions (Basari et al., 2014). The leader then stops and waits, setting off again only when the follower returns and antennates her (Möglich et al., 1974; Franklin, 2014). This process continues until the pair reaches the target (Figure 20.2). The follower then makes an independent assessment of the target (nest site or food source) and, depending on its quality, may return to the colony to lead her own tandem runs.



**Figure 20.1** A tandem running pair, with the leader at the right and the follower at the left, of *T. rugatulus*.



**Figure 20.2** Part of a tandem running path by a leader (black) and a follower (gray) (top) and their speed during the trip (bottom). The leader accelerates as the follower touches her, but the leader eventually slows down to allow the follower to catch up. When the follower breaks contact, the leader stands still until they are reunited (a and b points). This figure created based on *T. albigipennis* tandem running data collected by the authors

### What Social Information Is Transferred Through Tandem Running?

The most obvious information transferred by tandem runs is the location of valuable resources. During foraging, this sharing helps the colony to enhance its exploitation of rich food sources, and to adaptively allocate foragers across sources of different quality (Shaffer et al., 2013). During colony emigration, tandem runs help the colony reach consensus on a single nest site (Pratt, Mallon, Sumpter, & Franks, 2002). Since each tandem follower may herself begin recruiting, this generates a positive feedback cascade that builds up a corps of informed scouts who eventually begin transporting the bulk of the colony to its new home. During this later phase of emigration, transporters often lead tandem runs in the opposite direction (i.e., from the new nest site to the old) (Mallon, Pratt, & Franks, 2001; Pratt et al., 2002; Planqué, Dechaume-Moncharmont, Franks, Kovacs, & Marshall, 2007). The function of these “reverse” tandem runs is not fully known, but they may serve to activate more transporters, to reallocate transport effort when the emigrating colony is divided, or to share information about optimal routes.

It is generally assumed that a tandem run follower learns not only the location of a resource, but also how to get there (e.g., Franks & Richardson,

2006). That is, the follower is thought to learn a specific path from home to destination, most likely guided by visual landmarks along the route (Bowens, Glatt, & Pratt, 2013). If so, this leads to the prediction that followers who later travel on their own from home to the destination should take a route that resembles the one on which they were led. However, published data appear to suggest that followers do *not* learn the route from their leader (Franklin, 2014). For example, Franks and Richardson (2006) tracked the paths taken by tandem followers when they returned from the target back to the old nest. These paths did not match the routes on which they were led. Another study showed that when followers later led their own tandem runs, they also did not use the route on which they had been led (Franklin & Franks, 2012). These studies cannot be considered definitive tests, because they had either a small sample size or little variance of individual routes. Thus, they lacked statistical power to conclusively reject the hypothesis of route learning during tandem recruitment.

We recently conducted a new experiment showing that the follower indeed learns a route from the leader during tandem running (Sasaki, Danczak, Thompson, Morshed, & Pratt, 2020). This experiment included two principal modifications of previous studies. First, we used a larger experimental arena (30 × 50 cm) than those used in previous experiments (e.g., 23 × 23 cm in (Franklin & Franks, 2012)) and supplied it with many visual and tactile landmarks, which were not provided in previous studies of route learning during tandem running (Franks & Richardson, 2006; Franklin & Franks, 2012; Franklin, Robinson, Marshall, Sendova-Franks, & Franks, 2012; Franklin, 2014). This gave us larger variation in individual routes, thus increasing our ability to detect consistent differences in the routes taken by different ants. Second, we measured route similarity using a more precise method originally developed to detect route stereotypy in homing pigeons over repeated releases from the same site (Meade, Biro, & Guilford, 2005; Guilford & Biro, 2014). In this method, route similarity is calculated as the average of nearest distances between points on the two routes (see Guilford & Biro, 2014 for details). Using these approaches, we were able to show that a tandem run follower subsequently uses a route more similar to the one on which she was led, compared to those of other tandem runs in the same emigration. This result shows that followers learn specific route information from their leaders during tandem running.

### **Studying Social Learning Using Tandem Running *Temnothorax* Ants**

Tandem recruitment's role in collective behavior, as well as its ability to transfer detailed route information, opens up new avenues of research about social learning's influence on collective intelligence. It should be noted

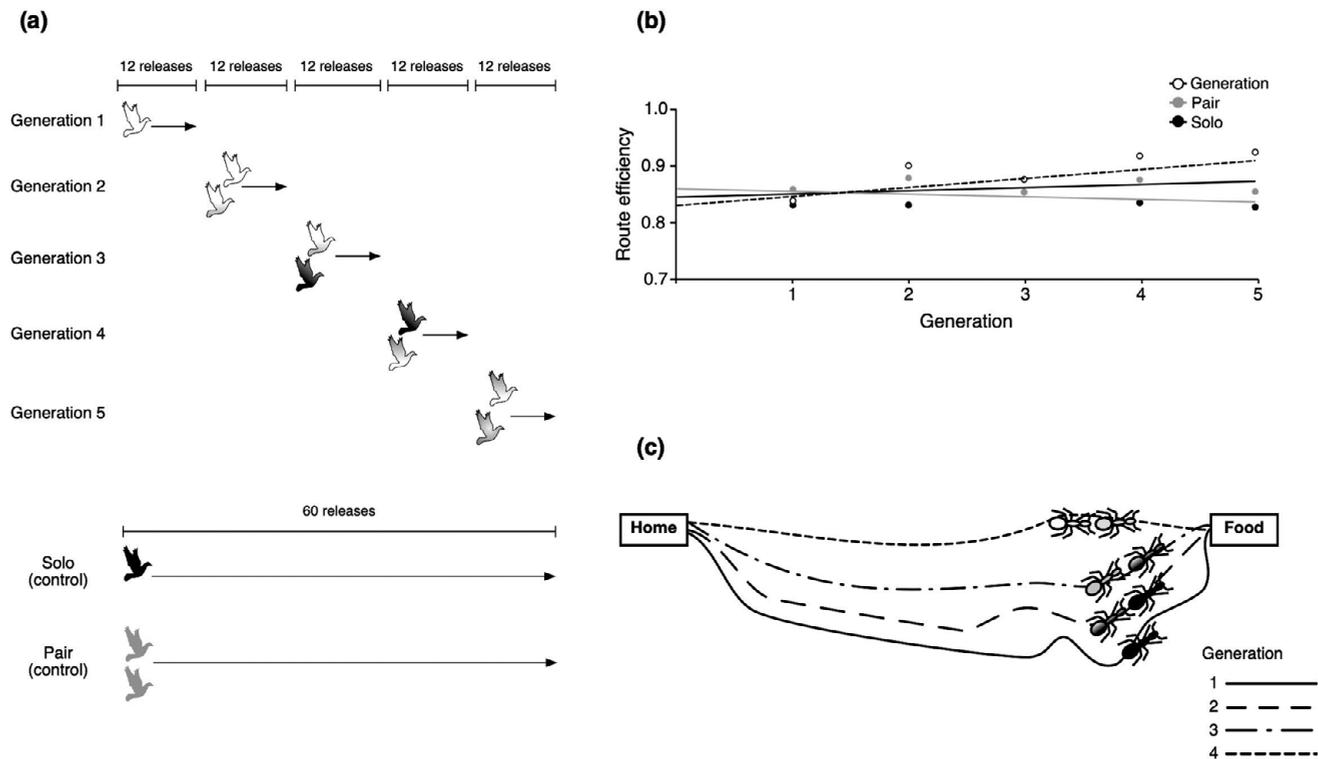
that tandem running is not the only recruitment behavior that conveys route information and plays a role in collective intelligence of social insects. For example, the better-known method of pheromone trails, widespread in ants, underlies collective decision making and also guides followers on precise paths (Detrain & Deneubourg, 2008; Czaczkes, Grüter, & Ratnieks, 2015). However, information spreads rapidly and anonymously on trails, making it difficult for an observer to track its dynamics. In contrast, each tandem run is a slow and readily observable dyad. Thus, we can directly detect who are the sender and the receiver of social information and how the information spreads in the colony, affecting collective performance over time. These advantages can facilitate progress on the research questions outlined below.

### Cumulative Cultural Evolution in Ants

Research on collective intelligence typically focuses on one-off performance, assuming that collective decisions are not influenced by information acquired from past experiences. Because animal groups in nature often face the same tasks repeatedly, feedback from past outcomes has the potential to influence their decision-making behavior (Biro et al., 2016). In fact, human groups are known to accumulate knowledge through individual invention and subsequent social learning and to improve collective performance over time, a phenomenon known as Cumulative Cultural Evolution (CCE) (Boyd & Richerson, 1988; Tomasello, Kruger, & Ratner, 1993; Tennie, Call, & Tomasello, 2009; Dean, Vale, Laland, Flynn, & Kendal, 2014). A recent study shows, for the first time in nonhuman animals, that pigeons progressively improve their homing routes over successive generations of repeated removal and replacement of individuals, demonstrating CCE (Figure 20.3a, b).

We hypothesize that *Temnothorax* ants may show CCE similar to that of pigeons. The first criterion for CCE is that individuals socially learn from others, as pigeons do from group leaders during homing. As noted above, this criterion is met in *Temnothorax*, where tandem run followers subsequently take a route similar to the one on which they were led. If the ants do show CCE, then we expect them to meet two other criteria: (1) their route efficiency should improve (i.e., travel distance should decrease) over a succession of tandem runs (Figure 20.3c) and (2) the chain of tandem runners should eventually outperform individual foragers who make the same number of trips (Dean, Kendal, Schapiro, Thierry, & Laland, 2012).

If *Temnothorax* ants demonstrate CCE, this could lead to novel insights about the underlying mechanisms. CCE is typically believed to emerge in populations with rare innovators and many social learners (Boyd & Richerson, 1988; Henrich, 2004), but research on homing pigeons shows that innovations can emerge through social interactions (Sasaki & Biro, 2017). That is, instead of the traditional view that superior innovations spread in a group via social learning (Boyd & Richerson, 1988; Henrich, 2004), we suggest that such



**Figure 20.3** CCE in homing pigeons and ants. (a) Experimental design for testing CCE in homing pigeons. In each chain of the experimental group (above), a single pigeon (white) was first released from the same site repeatedly twelve times, then partnered with a naïve pigeon (light gray) and flown as a pair a further twelve times. The first bird was then replaced by a third bird (dark gray) and this new pair (light gray + dark gray) was also released twelve times. This procedure continued until the fifth-generation bird was added and flown a final twelve times. In the control groups (below), single pigeons and fixed pairs were released the same number of times as the total flown by the experimental group (sixty flights). (b) Homing efficiency (measured as the beeline distance between release and home divided by the length of the path flown) for all flights in the experimental group (dotted line with open circles), the solo control group (black line with filled circles), and the fixed-pair control group (gray lines with gray circles). The final (twelfth) flight of each generation in the experimental group and the equivalent (twelfth, twenty-fourth, thirty-sixth, forty-eighth, and sixtieth) flights in the control groups are shown. While the route efficiency did not change over releases in the control groups, it progressively improved over generations in the experimental group. (c) A potential case of CCE in tandem running ants. By transferring route information through tandem running, they may collectively improve route efficiency, like homing pigeons. (a) and (b) are adapted from (Sasaki & Biro, 2017)

innovations can emerge through social learning (Biro et al., 2016). Integration of the fields of collective intelligence and CCE using *Temnothorax* ants as a model can elucidate how animals, especially ones with limited cognitive abilities, can progressively improve their collective performance over time.

### **Collective Optimal Foraging by Tandem Running Ants in an Unstable Environment**

Extensive empirical studies have shown how ants use recruitment to make adaptive decisions among food sources, and to develop optimal foraging routes among multiple sites (Buhl et al., 2009). Mathematical models have further demonstrated how these abilities emerge from the properties of recruitment behavior, and these insights have spawned computational approaches to the solution of analogous problems in transport, telecommunications, and other fields (e.g., Dorigo & Stützle, 2004). Nearly all of this work has been on ants that recruit via pheromone trails, but tandem recruitment may offer new lessons about optimization of foraging. This is because tandem running and trail laying differ in important ways, such as tandem running's slower speed, its one-to-one rather than one-to-many structure, and its close integration of chemosensory, tactile, and visual components of communication and navigation.

A key factor that has already been investigated is the functional relationship between recruitment effort and recruitment effectiveness. In trail-laying ants, this relationship is highly nonlinear, such that a doubling of trail pheromone concentration more than doubles the number of recruits delivered by the trail to a resource. Tandem runs, in contrast, are linear, such that doubling the number of tandem leaders simply doubles the number of recruits (Shaffer et al., 2013). This subtle difference has notable effects on collective performance. When faced with a choice between identical food sources, trail-laying species such as *Lasius niger* randomly choose one on which they concentrate their foraging effort (Detrain & Deneubourg, 2008), while *Temnothorax* colonies equally exploit both (Shaffer et al., 2013). More significantly, *Temnothorax* perform better in a fluctuating environment; that is, they are better able to redirect their foragers to a newly available better food source than are trail-laying ants (Shaffer et al., 2013). Thus, differing mechanisms of recruitment may be more suitable for different circumstances. The observable recruitment behavior of *Temnothorax* makes it easier to combine empirical studies with precise mathematical models. This approach can be used to explore tandem recruitment's contribution to how colonies optimally allocate foragers among variable food sources and how they develop foraging routes among them.

### **Context Effects on Social Learning During Tandem Running**

*Temnothorax* use tandem running during both foraging and colony emigration. In the latter context, as noted above, tandem runs are seen in both

directions: “Forward” tandem runs go from the old nest to the new nest in the early phase of emigration, while “reverse” tandem runs go in the opposite direction later in the emigration. The function of tandem runs may vary in these different contexts, and so may the information that is transferred. Because the tandem running behavior appears to be the same, it is easy for us to assume that followers learn a route from leaders in all tandem runs. However, this may not be the case. For example, in *Temnothorax albipennis*, the leader lays a pheromone during forward tandem running, but not during reverse tandem running (Basari et al., 2014). This additional cue could affect tandem follower behavior, although how it does so is still ambiguous. It might help the follower navigate, so that she can pay more attention to landmarks during forward tandem running, or she may learn less because she instead pays close attention to the pheromone.

If context affects what the follower learns, how might this affect collective performance? A mathematical model shows that, even if the follower does not learn a route, reverse tandem running can still improve emigration speed by increasing the recruitment workforce (Planqué et al., 2007). Furthermore, foraging and emigration differ in their collective goals: For the sake of colony cohesion, consensus on a single home is vital during emigration (Stroeymeyt, Giurfa, & Franks, 2010), but for foraging optimal allocation across multiple food sources may be more appropriate (Detrain, Deneubourg, & Pasteels, 1999). Therefore, tandem followers of foragers may learn routes less precisely than those of nest-site scouts, thus increasing their chance of random encounters with new food sources. In fact, such “errors” have been shown to be important for optimal foraging in trail-laying ants (Czaczkes & Heinze, 2015). Recent improvements in automated tracking systems will enable researchers to reveal if tandem followers acquire the same kinds or amounts of information in different contexts and how this affects collective performance.

### **Optimal Social Information Use as a Group**

Is it always better to use social information? In the restaurant example mentioned above, asking others for recommendations seems like a good strategy. However, this is not always the case. At one of the restaurants suggested by a colleague, the food turned out to be awful. The colleague later revealed that he had not been there for years, and a new owner had changed the menu quite a bit. Social information is not always accurate, perhaps because it is out-of-date or because the informant makes an error. Thus, if many group members rely on social information, the group can get stuck with a suboptimal option. This is a key limitation of social learning (Giraldeau, Valone, & Templeton, 2002) that poses a cooperation problem –

individual learners are cooperators who pay some cost (e.g., time and money) to introduce new information to their group, while social learners are defectors who take advantage of that “free” information (Rogers, 1988). Researchers have used human subjects and computer simulations to investigate how the introduction of individual learners to the group can improve collective performance (Kameda & Nakanishi, 2002, 2003; Rendell et al., 2010). A major research challenge is to understand when and how the tension between individual- and group-level fitness effects can be resolved in favor of the evolution of costly individual learning. Past research has shown that humans often selfishly rely on social information, and their group performance typically declines over time (Kameda & Nakanishi, 2003).

For social insects, information sharing is less of a cooperation problem. In their highly integrated societies, each individual’s best strategy for maximizing inclusive fitness lies in helping the success of the colony as a whole, rather than her direct reproduction (Seeley, 1989; Visscher & Camazine, 1999; Camazine et al., 2003; Pratt, 2005; Gordon, 2010; Grüter et al., 2010). This contrast to human groups offers a clearer view of the optimal way to allocate effort to individual vs. social learning so that collective performance actually increases over time.

## Conclusion

We have reviewed the potential of tandem running recruitment by *Temnothorax* ants to serve as a model system for understanding social learning. A key advantage is that each instance of information sharing – each tandem run – can be easily observed. Moreover, the specific information transferred can be readily inferred by tracking the history and subsequent behavior of leader and follower. In research to date, these advantages have shown how information sharing allows the emergence of collective intelligence. We have outlined new lines of investigation that further integrate collective intelligence with social learning, to answer questions about cumulative improvement over time, collective optimal forging in an unstable environment, context effects on the nature of information sharing, and optimal social information use as a group. Results from future studies can be compared with predictions made by past theoretical work on optimal social information use (e.g., Rendell, Boyd, et al., 2010; Rendell et al., 2011). In this way researchers can investigate whether social insects maximize collective performance by optimally sharing information and, if so, how they achieve this. We hope that the advantages of *Temnothorax* ants as a model system will allow the closer integration of the fields of collective intelligence and social learning, so that research may decipher how superior collective performance emerges from local interactions of group members.

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