Kulkarni Venugopal Vasant Word Count: 1072

NST2064: Social Insect Societies

Dr. Sebastian Pohl

AY2025/2026 Semester 1

Takes Two to Tandem

A foraging ant discovers a dead cricket too large to carry alone. Without language or technology to communicate its location, how does she mobilise help from nestmates hundreds of body lengths away? Many ant species solve the challenge of recruitment through mass communication, laying chemical trails that simultaneously guide dozens of workers to the target. Some ants employ social carrying, where workers physically transport nestmates to destinations. Yet many ant species have independently evolved a different, seemingly inefficient, strategy: tandem running (Glaser & Grüter, 2022).

During tandem running, an informed leader guides a single naive follower to a destination through a combination of tactile and chemical signals (Franklin, 2013). The follower maintains intermittent physical contact by tapping the leader's with its antennae, prompting the leader to move forward a short distance before pausing for the next tap (Schultheiss et al., 2015). Usually, this process dramatically slows both ants. For example, in *Camponotus consobrinus*, tandems travel at 2.7 cm/s compared to 5.6 cm/s for solitary foragers (Schultheiss et al., 2015). Moreover, these tandem runs frequently fail. In *Pachycondyla striata*, only 75% of tandem runs successfully guide followers to food sources (Silva et al., 2021). Even when runs succeed, they demand heavy opportunity costs as leaders devote time to escorting instead of foraging.

Why then would natural selection favour a recruitment method that moves at half speed, recruits only one worker per trip, and has frequent failures? Tandem running thrives in situations where small colony sizes limit mass recruitment and where the navigational knowledge gained through learning outweighs the costs of slow, failure-prone guidance.

The first context where tandem running excels emerges from colony size constraints. Small colonies face fundamental limitations in maintaining pheromone trails. Beekman et al. (2001) demonstrated that *Monomorium pharaonis* colonies require a critical mass of workers before pheromone trails can form. Below this threshold, volatile chemicals dissipate faster than a small workforce can replenish them. Mathematical models by Planqué et al. (2010) predict that different recruitment strategies become advantageous at different colony sizes, with tandem running being particularly suited to small to medium sized colonies. We see this in *Temnothorax nylanderi*, where colonies averaging just 130 workers maintain tandem run success rates around 80%, with experienced leaders achieving 94% success (Glaser & Grüter, 2018). For these small colonies, the reliability of tandem running is crucial as each worker represents a significant fraction of the total workforce. Colonies cannot afford the losses that occur when workers follow weak pheromone trails to nowhere. The assured guidance of tandem running - despite its slower pace - might become more valuable than the speed of mass recruitment.

The second advantage of tandem running lies in its unique capacity to "teach" that fundamentally differs from other recruitment methods. Franks and Richardson (2006) argue that tandem running qualifies as teaching because it often involves bidirectional feedback. For example, Richardson et al. (2007) found that in *Temnothorax albipennis*, leaders adjust their behaviour when a tandem run is interrupted by evaluating its follower, while followers actively learn by following the journey of the leader themselves. This contrasts with the honeybee waggle dance, which encodes distance and direction through symbolic movements but provides no further hand-holding - dancers merely "tell" recruits where to go without showing them how to navigate the terrain.

This distinction matters for colony efficiency. Sasaki et al. (2020) demonstrated that when former followers in *Temnothorax albipennis* repeated routes themselves, they showed significant similarity to their original journey, replicating specific navigational decisions. It is hypothesised that the ants are able to memorise visual cues along the route they are led on, with tandem running effectively serving as a means of transferring this knowledge at a faster rate than it would be gained by foraging individually (Franklin & Franks, 2012; Sasaki et al., 2020). It is not surprising then, that even failed tandem runs provide value. Ants that participated in unsuccessful tandems still show higher success rates in eventually reaching the destination compared to ants that never experienced tandem running at all. For example, Pratt (2008) found that lost *Temnothorax curvispinosus* followers found new nests three times faster than ants that were never part of a tandem. This suggests that even partial exposure to the route during a failed tandem provides valuable navigational information. This learning aspect has the potential to become particularly valuable in complex or changing environments. While pheromone trails fade or environmental conditions shift, the information acquired through tandem running persists, allowing colonies to maintain foraging efficiency even when chemical communication systems fail.

However, tandem running faces severe limitations when foraging distance and time become critical factors. Pratt (2008) found that *Temnothorax curvispinosus* tandem runs failed 70% of the time at 65 cm versus 43% at 11 cm, showing how distance degrades success rates. Even when *Temnothorax nylanderi* maintained similar success rates across distances from 7 to 28 cm, followers at greater distances searched 82% longer after breakups before giving up, and successful tandems took proportionally longer to complete (Glaser & Grüter, 2018).

These distance and time related costs matter when considering resource competition. Agent-based models by Goy et al. (2021) suggest that tandem running becomes disadvantageous when colonies compete for short-lived food sources. Solitary foraging consistently outperformed tandem running, as the time invested in slow recruitment allowed solitary foragers to monopolise resources before tandem-running ants could mobilise sufficient workers. The *Cataglyphis* desert ants may exemplify this trade-off, relying entirely on individual foraging for the small arthropods that single workers can transport independently (Steck et al., 2009). Here, the time investment in tandem running is likely unnecessary when solitary retrieval suffices.

At first glance, tandem running might look slow, and unreliable. Indeed, it was once believed this recruitment method was “primitive” (Franklin, 2013). Yet as we see in this essay, this behaviour has its advantages. For small colonies, it offers a reliable way to get help when pheromone trails would simply vanish. Tandem running also acts as a form of “teaching”, giving young workers the chance to learn the routes and landmarks they will need for future foraging. Even failed tandems leave recruits better prepared than before. In this way, tandem running trades speed for resilience, equipping colonies with a memory-based navigation system that endures even when trails fade or environments change. Its survival across so many species shows that natural selection does not always favour the fastest or most efficient solution, but the one best matched to a colony’s size, needs, and environment.

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