

The Evolution of Honey Bee Communication: Learning from Asian Species

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ABSTRACT

Asian honey bees provide fascinating insights into the evolution of honey bee foraging communication. Although all honey bees use the waggle dance to communicate resource location, variations in the waggle dance and in the biology of Asian species have led to several different hypotheses about how and why this famous behavior evolved. In this review, my goal is to suggest areas of research and questions that will help us understand the evolution of honey bee foraging communication in greater detail. Specifically, I would like to draw attention to the selective pressures imposed by direct competition and aggression over floral resources and nest robbing, signals related to danger, and experiments that may allow us to resolve questions about honey bee dance dialects. I hope that these suggestions will stimulate more research in Asian honey bees and allow us to develop a better overall picture of the evolution of foraging communication in the corbiculate bees (Hymenoptera, Apidae).

Key words: dance language evolution, competition, foraging, communication, danger signals

Introduction

Honey bees are an important model for the study of animal communication because they use functionally referential communication to encode the distance and direction to a food source (von Frisch, 1967). As Karl von Frisch aptly stated, this system has been a “magic well” for Behavioral Ecologists and Neuroethologists, continually providing important new insights

(Giurfa, 2007). Biologists know the most about one species, *Apis mellifera*, and it is therefore encouraging to see growing interest in other species of honey bees (Hepburn and Radloff, 2011). The famous honey bee waggle dance and the variations that exist in different species have been recently well reviewed (Duangphakdee *et al.*, 2011). Therefore, my goal is not to provide a comprehensive survey, but to select a few threads in this fascinating

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story that would be profitable to investigate. I would like to increase our understanding of *why* and *how* honey bee recruitment communication has evolved by stimulating research in specific areas.

The exact number of honey bee species is debated, but many taxonomists recognize nine species: the dwarf honey bees (*A. andreniformis* and *A. florea*), the medium sized bees (*A. mellifera*, *A. cerana*, *A. koschevnikovi*, *A. nigrocincta*, and *A. nuluensis*), and the giant honeybees (*A. dorsata* and *A. laboriosa*) (Radloff *et al.*, 2011). I will focus on the Asian honey bees, primarily *A. florea*, *A. andreniformis*, *A. dorsata*, and *A. cerana*. It should be noted that *A. cerana* behaviors described in the literature may also apply to *A. koschevnikovi*, *A. nigrocincta*, and *A. nuluensis* given that recognition of these other species is relatively recent (Radloff *et al.*, 2011).

Selective pressures

Researchers have focused on two selective pressures influencing honey bee foraging: (1) the spatial distribution of food sources and (2) competition. Rich, clumped food sources can be valuable to recruit for (mass foraging), whereas more dispersed food sources may be better exploited by individual foragers that do not recruit to a specific location (Dornhaus 2002). In *A. mellifera*, colonies in temperate habitats (less clustered food) in which waggle dance location information was eliminated, gained the same weight as controls. However, colonies in an Asian tropical forest with more clumped food resources (determined from undisturbed waggle dances), gained significantly less weight when waggle dance location information was eliminated (Dornhaus and Chittka, 2004). In addition, the role of resource spatial patchiness has been modeled, demonstrating the theoretical advantages of location communication for rich clumped food sources (Dornhaus *et al.*, 2006).

How competition has shaped honey bee

foraging communication is less well understood. Honey bees are foraging generalists that collect nectar and pollen from a wide variety of species (Michener, 1990). There is evidence for ecological niche overlap among Asian honey bees. For example, *A. florea* and *A. dorsata* visit many of the same floral species (Abrol, 2011). Although *A. mellifera* is an introduced species in Asia, it is now in competition with native species, likely adding to competition that already existed among native species. For example, experimental removal of *A. mellifera* increased the number of *A. cerana* visiting four crop plants (Partap *et al.*, 2000). Honey bees can reduce such competition by foraging at different times. The flowers of *Pterocarpus santalinus* open at midnight and are visited extensively by *A. dorsata* on moonlit nights from midnight until dawn. *Apis cerana* and *A. florea* visit only during early morning hours, competing with each other, but avoiding direct competition with *A. dorsata* (Rao and Raju, 2002).

Honey bees can avoid competition by foraging on different plant species. *Apis florea* will visit species whose flowers provide low caloric rewards whereas *A. dorsata* prefers flowers with high caloric rewards. *Apis florea* visited several species such as *Daucus carota*, *Allium cepa*, and *Trigonella foenumgraecum* that were not visited by *A. dorsata*. However, specialized attraction may not always relate to caloric rewards. *Apis florea* was more attracted to *Brassica campestris* blossoms, even though these were less rewarding than *Cajanus cajan* flowers (Sihag and Rathi, 1992). In addition, different floral nectar compositions are favored by different species (Abrol, 2011). Species can also avoid competition by foraging under different environmental conditions and at different times of day (Abrol, 2011).

Conflict and aggression

When multiple species simultaneously forage on the same resource, conflicts can

occur. For example, *A. florea* exhibited aggression towards *A. mellifera* on flowers (Chahal *et al.*, 1986). *More studies that examine aggression and conflict among native Asian species at natural food sources would be highly useful.* However, research using artificial feeders and a mixture of native and introduced species (mainly *A. mellifera*) is still revealing. When *A. mellifera* and *A. cerana* were trained to separate sucrose feeders (50% sucrose w/w) that were gradually brought closer together, aggression arose. Ultimately, *A. mellifera* were dominant and completely excluded *A. cerana* (Dhaliwal and Atwal, 1970). At sugar water feeders, researchers found an aggression hierarchy among different Asian species. *Apis florea* was dominant over *A. cerana*, which was dominant over *A. dorsata*. *Apis florea* attacked *A. cerana* 13 fold more times than vice versa and *A. cerana* attacked *A. dorsata* 3 fold more times than vice versa. Conspecific aggression also occurred between *A. cerana* colonies (Koeniger and Vorwohl, 1979). Similarly, Ruttner (1988) found that *Apis dorsata* was attacked by *A. cerana*, not by *A. florea* or *A. mellifera*. At an artificial sucrose feeder, *A. florea* and *A. cerana* could dominate the feeder, excluding the larger *A. dorsata* and chasing off other species. In this study, *A. florea* and *A. cerana* foraged together without exhibiting aggression (Ruttner, 1988). Overall, small-bodied species exhibited more aggression and were dominant relative to larger-bodied species.

This hierarchy is counterintuitive because the larger individual usually beats the smaller in animal contests (Alcock, 2001). However, in social insects, the ability of the colony to recruit large numbers of individuals plays a role. We can apply the concept of the contestant size to superorganism (colony) size, not merely the size of an individual forager. A colony that can mass recruit a larger number of smaller-bodied workers can win against a fewer number of larger-bodied ones (Lichtenberg *et al.*, 2010). Nonethe-

less, it is fascinating that in one-on-one contests a smaller bee can win over a larger one (Koeniger and Vorwohl, 1979; Ruttner, 1988). This phenomenon is widely observed in stingless bees (Johnson, 1974; Johnson and Hubbell, 1974; Roubik, 1978; Roubik, 1981; Johnson, 1983; Nagamitsu and Inoue, 1997; Nieh *et al.*, 2005). One explanation is that smaller species are more limited in flight range than larger species (Greenleaf *et al.*, 2007). Therefore, the smaller-bodied species invest more effort and will take greater risks when fighting to defeat a larger-bodied species, which can abandon the contested patch to search for one further away (Koeniger and Vorwohl, 1979).

A more complete understanding of social bee competition for floral resources should also include other bees, particularly the stingless bees, which can exhibit high levels of aggression and displace honey bees on natural food sources (Nagamitsu and Inoue, 1997). Apis koschevnikovi and stingless bees visited honey water feeders placed at different heights in towers (Nagamitsu and Inoue, 2005). In a separate experiment, stingless bees attacked A. koschevnikovi at honey water feeders, but A. koschevnikovi never exhibited aggression against stingless bees (Nagamitsu and Inoue, 1997).

Honey bee nests provide rich resources. Inter- and intra-specific nest robbing can therefore occur, particularly when a colony is poorly defended. *Apis indica* and *A. mellifera* colonies can rob each other, depending on which colony is weak (Atwal and Dhaliwal, 1969). In an apiary containing both *A. cerana* and *A. mellifera*, *A. cerana* initiated robbing of *A. mellifera* colonies more than vice versa, but *A. cerana* colonies were more likely to die during conflicts with *A. mellifera* colonies (Yang *et al.*, 2011). Among native Asian species, robbing occurs between *A. dorsata* and *A. cerana* (Atwal and Dhaliwal, 1969). In some cases, robbing by *A. dorsata* can reduce the survival of *A. indica* colonies

(Singh, 1959). As with floral food competition, the extent of nest robbing among sympatric native *Apis* species is poorly understood. *It would be useful to determine the patterns of interspecific nest robbing among different native species of Asian honey bees. Is there a hierarchical pattern, similar to a dominance hierarchy, in how species interact during nest robbing?*

The mechanisms that allow certain species to win fights against others remain poorly understood. In fights over a feeder, A. mellifera stung and killed A. cerana. (Dhaliwal and Atwal, 1970). However, during intraspecific fights between A. mellifera foragers over an artificial feeder, I have rarely observed stinging. The primary mode of A. mellifera attack, as in stingless bees, involves biting (Nieh et al., 2005; Lichtenberg et al., 2010; Nieh, 2010). Thus, species may adopt different attack strategies depending upon the competition. At nests, A. florea displaced A. mellifera on comb and fought with A. mellifera guards to rob their nest (Chahal et al., 1986). Although A. mellifera guards bit and pulled at the robbers on their legs, wings, and other body parts, A. florea often managed to escape.

How they did so is unclear, but understanding their ability to escape may explain how they eventually won and successfully robbed the colony. Apis florea was able to sting and avoid being stung. Out of 124 dead A. mellifera, 14% had been stung by A. florea, but 0% of A. florea had been stung by A. mellifera (Chahal et al., 1986). Interestingly, once the colony had “submitted” there was relatively little resistance from the invaded A. mellifera (Chahal et al., 1986). This is reminiscent of the behavior of a stingless bee colony that initially fights and then retreats when invaded by the robber stingless bee, Lestimelitta limao (Sakagami et al., 1993). This phenomenon of “submission,” how it occurs, and what triggers it would be fascinating to study. From the perspective of the superorganism, how is the consensus

to cease fighting achieved?

Signaling about danger

In general, the effects of competition and fighting on food recruitment communication are not well understood. This is a part of the evolutionary story that remains to be fully explored. There is evidence for negative feedback signaling that counteracts the positive feedback produced by recruitment dances. During competition for a feeder, *A. mellifera* foragers that were attacked, returned to the nest and produced “stop signals.” The stop signal is a brief vibrational signal lasting around 150 ms (Kirchner, 1993) at 380 Hz (Michelsen et al., 1986) and is frequently delivered by a sender butting her head into a recipient, most frequently waggle dancers (Nieh, 1993). The stop signal or “brief piping signal” (Seeley and Tautz, 2001; Thom et al., 2003) was originally described as a food begging call (Esch 1964; von Frisch 1967). However, it does not elicit food exchange (Nieh, 1993; Pastor and Seeley, 2005). Instead, it causes waggle dancers to stop dancing and leave the nest (Kirchner, 1993; Nieh, 1993; Pastor and Seeley, 2005). Bees produce stop signals under natural conditions and signal recipients waggle dancing for natural resources will reduce their waggle dancing (Pastor and Seeley, 2005). Natural and synthesized signals significantly increased waggle dancer departure (Nieh, 1993). Stop signal playbacks reduced waggle dance durations by 59% and recruitment by 60% (Kirchner, 1993). In addition, deteriorating foraging conditions (crowding or increased feeder wait time) increase stop signal production (Thom et al., 2003; Lau and Nieh, 2010).

During competition for a rich food source, *A. mellifera* competitors attacked resident bees. Bees that were attacked (victims) increased the number of stop signals by 43 fold and sharply decreased (by 12.6 fold) the number of waggle dance circuits performed. Bees that were undi-

sturbed (received and gave no attacks) and bees that attacked competitors continued to recruit and produced almost no stop signals (Nieh 2010). In addition, signalers targeted bees that smelled like the odor at their feeding location. The proximate causes of stop signal production can be further broken down into receiving physical aggression (biting) and detecting alarm pheromone. (Nieh, 2010).

There is a benefit to such a signal. Each individual forager decides on whether and how much to recruit. However, one individual's decision to cease recruiting does not stop recruitment by other waggle dancers. By sending stop signals, she can inform foragers visiting the same location of adverse foraging conditions and give negative feedback to counteract waggle dancing by others. Broadly, collective foraging of the superorganism arises from the positive and negative feedback of multiple agents, with negative feedback cycles evidently providing greater precision and speed for labor reallocation. *Whether this occurs in other species of honey bees, particularly Asian species, is unknown. However, given the evidence for interspecific aggression at floral resources and during nest robbing, Asian species of honey bees may also have the stop signal. A comparative analysis could help us to understand how this signal functions and how it may have evolved.*

The stop signal is related to the experience of danger at a food source, and falls within a larger class of movement and vibrational signals related to danger. It would therefore be informative to examine other danger-related signals and see if they share common features. Several defensive behaviors (some of which may be signals) could be better understood. Defensive hissing signals are one example. Butler (1954) described a combined body shaking and hissing in *A. cerana*. *Apis mellifera cypria* produces high frequency hissing sounds when being attacked by the hornet, *Vespa orientalis* (Papachristoforou

et al., 2008). Such hissing has not been reported in other subspecies of *A. mellifera*, although they are also attacked by wasps. *Apis florea* workers produce a hissing sound during nest defense, combined with slight wing movements. These behaviors spread to nearby bees and may deter certain predators (Sarma *et al.*, 2002). *It would be informative to learn if other Asian honey bee species produce hissing sounds when attacked by predators.*

The nests of open nesting species are more exposed to predators than nest-cavity dwelling species. Open nesting species have thus evolved some interesting deterrents and signals. *Apis nuluensis* performs defensive shaking behaviors in response to hornet predators. This shaking recruited guards to the predator's location and also induced shaking in nearby bees (Koeniger *et al.*, 1996). *Apis dorsata* produces shimmering patterns consisting of adjacent bees flipping their abdomens upwards. This motion spreads throughout the comb surface in a wave-like pattern, and is stimulated by the presence of a predator, such as a wasp (Schmelzer and Kastberger 2009). Detailed video analyses show that wasps avoided the shimmering surface and were therefore prevented from directly capturing shimmering bees (Kastberger *et al.*, 2008). There may be specialization in which workers perform the shimmering, since it is primarily triggered in the area where foragers arrive, dance, and then depart (Schmelzer and Kastberger, 2009). Finally, drones are generally not thought to play a major role in colony defense. However, *A. cerana* drones reportedly participated in shimmering. Drone shimmering wing motions were less distinct than those of the workers, but were distinguishable (Sakagami, 1960). *Drone defensive behavior would be profitable to study because so little is known about what drones contribute to the colony, aside from their task of mating with virgin queens.*

What shapes the precision of location communication?

What constrains the precision of the waggle dance? There is a continuous transition between round dancing and waggle dancing: from dances that provide no or small amounts of location information to dances that provide precise distance and direction information (von Frisch, 1946; Gardner *et al.*, 2008). Interestingly, there can be substantial variation in the waggle phase angle (divergence angle), but this generally decreases as the distance to the resource increases (Towne and Gould, 1988). Two explanations have been proposed for this variance. *The adaptive hypothesis* states that this variance increases colony exploitation of resource patches by scattering recruits. Resources such as nectar or pollen typically occur in patches, not as points (unlike nest sites, Gould, 1975; Weidenmuller and Seeley, 1999). Therefore, the adaptive hypothesis predicts that waggle dances for nest sites should exhibit greater precision (less variance in waggle phase direction) than dances for food sources, at least for close distances. In the adaptive hypothesis, natural selection has shaped the divergence angle to improve colony foraging efficiency and nest migration.

The constraint hypothesis states that this variance results from sensory and performance constraints. Under this hypothesis, the divergence angle is not a specific adaptation shaped by natural selection in response to food source patchiness and house hunting. Rather, it arises from constraints on sensory mechanisms that bees use to orient their dances. The constraint hypothesis proposes that bees are “doing the best they can” given the conditions they experience while dancing. For example, *A. mellifera* foragers with visual references during dancing had a smaller divergence angle than when they were deprived of visual references (Tanner and Visscher, 2010). Since they normally have visual references while

dancing, the open-nesting Asian honeybees provide an interesting natural test of the importance of visual constraints in the dance language. For example, in *A. florea*, there was a lull between noon and 1:00 pm in absconding dances, perhaps because of increased difficulty in determining the sun’s azimuth when it was at its highest point in the sky (Atwal and Dhaliwal, 1969). In Iran, *A. florea* built combs in which the horizontal section was clearly exposed to blue sky, perhaps to facilitate orientation (Tigari, 1971).

Early experiments on open-nesting Asian species (*A. florea*, *A. cerana*, and *A. dorsata*) showed significantly smaller divergence angles than for *A. mellifera* at comparable distances (see Fig. 12 of Towne and Gould, 1988). However, Beekman *et al.* (2008) studied the spatial precision of *A. florea* waggle dances and found no significant differences between dance divergence angles for nest sites (point sources) and food sources (patches). Beekman *et al.* (2008) also found no significant difference between waggle phase durations (which provide distance information) for nest sites or food sources. Weidenmuller and Seeley (1999) studied *A. mellifera*, and likewise found no differences in waggle phase durations for nest sites or food sources.

However, Beekman *et al.* (2008) found an effect of distance on variance in waggle phase duration. In *A. florea*, variation in this distance information increased as the distance to the food source increased. Thus, as the distance to the resource increased, the distance information became less precise. This is different from what is reported for *A. mellifera*, where distance and direction information became more precise with increasing distance (Towne and Gould, 1988). Beekman *et al.* (2008) thus suggested that directional information may be more important than distance information in *A. florea*. This matches what is reported for *A. dorsata* workers dancing on the surface of a swarm for nest

sites (Dyer and Seeley, 1994). These dancers exhibited consistent directionality but highly variable waggle phase durations (mean waggle phase duration of 42 dancers was 20.8 ± 16.5 s, with a range of 6.4 to 72 s). In contrast, dances for food sources exhibited less variance in dance circuit duration. *Given the evident low level of waggle dance distance information in A. florea (for food sources) and A. dorsata (for nest sites), it would be useful to examine the precision of distance communication in these species using feeder or nest site arrays.*

Interestingly, the same increase in imprecision with increasing distances (putatively conveyed through the duration of recruitment sound pulses) is reported in the stingless bees, *Melipona panamica*, *M. mandacacia*, and *M. bicolor* (Nieh and Roubik, 1998; Nieh *et al.*, 2003). *Is there something about the habitat of tropical species that makes precise distance communication less important?*

In terms of the constraint hypothesis, studies on the effect of dancing on a vertical comb vs. a horizontal comb would be informative, as Beekman *et al.* (2008) suggest. Such dances occur naturally in *A. florea*, which has a relatively flat portion of the comb above the plant branch holding the nest. For this species, horizontal dancers should rely only upon vision for orientation whereas vertical dancers could use vision and gravity. Careful experiments with this species may reveal if there are sensory constraints on waggle dance precision. *One predicts that in A. florea, for any given location, waggle dancers using multimodal orientation information (vision and gravity: on vertical comb surface) should exhibit different divergence angles from dancers using single-modal visual information (on the horizontal comb surface).*

Selection on dance dialects and distance coding

If one plots the duration of the waggle

phase performed for any given distance, the duration of the waggle phase increases with increasing distance to the food source (von Frisch, 1967). The resulting curve is called the “dialect curve” or the “distance coding curve.” Has this dialect curve been shaped by the typical foraging range of a species? Some researchers have reported different codings of distance between honey bee species (Lindauer, 1956; Punchedewa, Koeniger *et al.*, 1985). These “dialects” may be shaped by species foraging ranges, based upon two assumptions. The first assumption is that steep dialect curves are more precise (providing a greater difference in signaling per unit increase in distance signaled). The second assumption is that the total steepness is constrained such that shorter maximum forager distances should correspond to steeper curves. Thus, species with different foraging ranges should have different distance codings. Early research reported that smaller-bodied species (with smaller forager ranges) had steeper dance dialect curves (Lindauer, 1956; Boch, 1957; Gould, 1982; Punchedewa, Koeniger *et al.*, 1985; Towne and Gould, 1988). More recently, Su *et al.* (2008) compared the distance curves for *A. cerana* and *A. mellifera* and found significant slope differences. They reported that the distance curve slope for *A. cerana* was significantly steeper than for *A. mellifera*.

However, Dyer and Seeley (1991) found no significant differences between the distance coding “dialects” of the different Asian species of honeybees (*A. florea*, *A. cerana*, and *A. dorsata*) although, based upon decoding dances for natural food sources, there were significant differences in flight ranges. The larger-bodied species, *A. dorsata*, had the largest foraging range (95% of dances were for distances estimated to be less than 3.8 km) compared to the smaller-bodied *A. florea* (1.3 km for the 95% point) or smaller-bodied *A. cerana* (0.9 km for the 95% point). The authors point out that observations over a variety

of seasons are required for a more robust test of the dance dialect tuning hypothesis (Dyer and Seeley, 1991). They conclude that their data may support the hypothesis of different dance dialects, but do not support the idea that dialects are strongly shaped by the maximum foraging distance of each respective species. They suggest that visual sensory constraints may explain why open nesting bees (*A. dorsata* and *A. florea*) have relatively long maximum dance circuit durations in comparison with *A. mellifera* and *A. cerana*, which nest in cavities.

Instead of examining the slope of the dialect curve, one can measure the transition distance from round to waggle dancing. Towne and Gould (1988) found differences such that *A. florea*, *A. dorsata*, and *A. cerana* transitioned to waggle dancing (called “oriented dances” in their paper) at much shorter distances (< 10 m) than *A. mellifera* (> 50 m). *Whether these Asian species actually use this waggle dance information at such close distances and how precise recruits are would be useful to determine.* However, Sarma *et al.* (2004) found no differences between the distances at which *A. mellifera carnica* and *A. florea* transitioned from round to waggle dances. Their paper introduces a useful technique of counting the number of circling runs and waggle phases. This avoids the problem of classifying the dance as either a round or a waggle dance, which can be difficult in borderline cases, and is a method that future studies may wish to use.

These differing results could arise if there is considerable intraspecific variation in the distance coding curves of each species. No studies, to my knowledge, have explicitly examined this by testing several colonies of the same species with the same procedures, but in different locations. Some intraspecific variation is expected. The distance at which a forager transitions from round to waggle dancing appears to be controlled by a single locus with

multiple alleles (determined in a genetic backcross with different strains of *A. mellifera* (Rinderer and Beaman, 1995; Johnson, Oldroyd *et al.*, 2002; Oldroyd and Wongsiri, 2006). Recently, genomic changes have been detected when individuals were forced to shift from foraging at perceived short distances to perceived long distances by manipulating optic flow (Sarma, Rodriguez-Zas *et al.*, 2010).

Another explanation for the dialect differences measured by some authors and the lack of strong dialect differences measured by Dyer and Seeley (1991), lies in the optic flow bees experienced in these different experiments.

Apis mellifera measures distance by measuring optic flow (Srinivasan, Zhang *et al.*, 1997; Srinivasan, Zhang *et al.*, 2000; Esch, Zhang *et al.*, 2001). This likely is the same for all *Apis* species, because at least one species of stingless bee (*Melipona seminigra*) uses optic flow to measure distance (Hrncir *et al.*, 2003), and one species of bumble bee (*Bombus impatiens*) can use optic flow during flight orientation (Dyhr and Higgins, 2010).

Given what we now know about the importance of optic flow in *A. mellifera* distance estimation, *it would be useful to test Asian species for distance dialect differences using optic flow tunnels that allow for more controlled comparisons.* Comparisons in natural habitats need to control for differences in optic flow that are perceived along the foraging route. For example, honey bees trained to fly through an optically dense habitat performed longer waggle phases than those trained to the same linear distance in a less optically dense habitat (Tautz, 2008). In general, it would be useful to check whether the Asian honey bees (1) also use optic flow to measure distance and (2) how their odometer is calibrated and compares with what is known for *A. mellifera*.

As an aside, more research on the vision of Asian honey bees would be beneficial, not only to better understand visual

resolution and parameters that influence the perception of optic flow, but also to understand the fascinating phenomenon of night foraging. *Apis dorsata* eyes have large ocelli and are more sensitive to dim light than those of other *Apis* species (Somanathan *et al.*, 2009). The bright yellow flowers of *Pterocarpus santalinus* open at midnight and are visited extensively by *A. dorsata* on moonlit nights (Rao and Raju, 2002). However, the waggle dances of *A. dorsata* are evidently oriented towards the unseen sun, not the moon (Dyer, 1985a). This raises the question of how these bees are able to avoid orienting towards a bright object in the sky (the moon) as a replacement for the sun, when *A. mellifera* generally accepts a bright object such as a lamp and uses this as a substitute “sun” (Gould, 1975). *Controlled experiments with A. dorsata colonies on moonless nights or in a darkened area and a light source of variable brightness could help to determine what levels of brightness this species finds acceptable as a substitute sun. It would be interesting to compare this threshold level of brightness with other species that do not forage at night.*

Finally, do dance dialect differences actually matter? How is recruitment precision affected? Tan *et al.*, (2009) created mixed colonies of *A. mellifera* and *A. cerana* and examined what happened when sender and receiver were the same or different species. They trained bees to feeder placed 130 m away within a linear array of four feeders. There were differences in the number of bees recruited by intra- or inter-specific recruits. Surprisingly, precision of communication (where recruits showed up) was not significantly different between same- or mixed-species pairs (Tan *et al.*, 2009) or in a similar experiment where foragers from mixed-species colonies were trained to a more distant, 500 m feeder array (Su *et al.*, 2008).

Conclusions

Much remains to be learned about why and how the honey bee waggle dance evolved and how, as a powerful force for positive feedback, it is countered by negative feedback communication.

In testing the importance of various selective factors, it is important to recognize that the *value* of recruitment and recruitment information varies with multiple factors such as colony need, the availability and patchiness of food sources in the environment (Dornhaus and Chittka, 2004), and the experiences of foragers (Grüter and Farina, 2009). Given this range of factors, it is perhaps not surprising that experiments are sensitive to small changes in methodology and to the motivation of and private information possessed by recruits. One example of this complexity is shown in the different classifications of foragers: scouts, reactivated foragers, and experienced foragers (Biesmeijer and de Vries, 2001). These categories reflect the motivation of individual bees to seek out certain types of information and food sources, and these like arise from a motivational continuum. This should increase variance in the different behavioral outcomes.

Recruiter motivation may also affect waggle dancing in more subtle ways, not just changing the number of dance circuits, but also varying how the dance is performed. Honey bees may not perform many waggle dances and can be very difficult to train to an artificial feeder (even a rich one) when there is abundant natural food. Whether the motivation to recruit also affects the accuracy of waggle dance information remains unclear, but it is known that waggle dances, at least in *A. mellifera*, can exhibit a wide range of variation and “excitement” from the classic “figure eight” to a forager that produces sporadic waggle phases interspersed by meandering around the nest (von Frisch, 1967). *Studies that examine*

this variation in detail would be illuminating, particularly by obtaining comparative data from the Asian honey bees.

In closing, I would like to note that several phylogenetic trees have been suggested for *Apis*. These different trees influence our hypotheses on how the waggle dance evolved. It is tempting to see in the waggle dance the ritualized path of a forager as she leaves the colony to collect food (waggle phase), returns to the nest to unload her collected food (return phase), and then returns to collect more food (waggle phase) again. The beautiful pattern of the waggle dance thus traces, in miniature, her foraging cycle (von Frisch, 1967). This analogy could be extended to the round dance, which occurs when the resource is close to the nest. Round dances can have a minor directional component (Gardner *et al.*, 2008), but largely consist of circular “return phases.”

We can call this scenario 1. In this scenario, the ancestral waggle dance pointed directly at the food source and was performed on a horizontal surface. Later, the complication of cavity-nesting (which provides no to very limited horizontal surfaces and limits visual orientation) led bees to dance on vertical surfaces, and thus the gravity-oriented vertical waggle dance evolved.

The real story may not be so elegant. The ability to dance on horizontal surfaces could be derived (scenario 2). In scenario 2, based upon molecular analyses and the cavity-nesting habits of all Euglossini, all Bombini, and most Meliponini, the *Apis* ancestor was a *cavity nesting species*. All cavity nesting species build vertical honeycombs. All honey bees species waggle dance, and thus the ancestral *Apis* likely performed the waggle dance on a vertical comb (Koeniger *et al.*, 2011). The small honey bees, *A. florea* and *A. andreniformis*, would then have evolved to nest on branches, where they have a horizontal component to their comb (the part above

the branch) and a clear view of visual markers such as celestial cues to orient an evolutionary innovation, horizontal dances.

Interestingly, *A. florea* seems unable to use gravity orientation for waggle dancing and lacks some of the gravity receptors found in other *Apis* species (Jander and Jander, 1970). When *A. florea* foragers are forced to dance on a vertical surface, such as formed by a swarm, or in experiments in which the comb is rotated, they will dance such that their waggle run points at the goal, not with reference to gravity (Dyer, 1985b). Instead, visual stimuli play an important role. Koeniger *et al.* (1982) found that *A. florea* dances on the horizontal surface of the comb were affected by an image of sky seen through a mirror.

The cavity nester, *A. mellifera*, can also perform oriented dances on a horizontal surface when they have a sky view. *It is unclear whether A. dorsata or A. cerana can perform oriented dances on a horizontal surface, although this would be interesting to determine. Surprisingly, the literature is, to the best of my knowledge, silent on this question.* If *A. dorsata* and *A. cerana* can dance on horizontal surfaces, pointing in the direction of the resource, one parsimonious, though somewhat unsatisfactory answer, is that the ancestral *Apis* could dance on a horizontal surface and on a vertical surface (scenario 2). Alternatively, if we adopt scenario 1, *Apis* first evolved horizontal dances that pointed directly at the food source and then evolved vertical dances, *but never lost the ability to perform horizontal dances*. Thus, the existing species of *Apis* may not provide definite information about how the waggle dance evolved. However, detailed studies of what these species are capable of will still be valuable for understanding the communication of these fascinating organisms.

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