

## **Waggle dance behavior associated with seasonal absconding in colonies of the African honey bee, *Apis mellifera scutellata***

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### **Summary**

Waggle dance activity associated with seasonal absconding (migration) was investigated in two colonies of the African honey bee. Prior to absconding, waggle dances regularly communicated distances up to 10–20 km from the nests. However, compared to waggle dances observed during nonabsconding periods, those occurring prior to migration were less associated with food sources, occurred during periods of little or no flight activity, and exhibited great variability in the communication of distance by consecutive waggle runs of individual bees. It is therefore unlikely that “migration dances” communicated the locations of, or stimulated immediate recruitment for, specific foraging or nesting sites. Rather, the dances may have functioned to establish a general route of travel. The majority of migration dances observed were oriented in an easterly direction, and upon departure both colonies traveled towards the E-SE. The orientation of migration dances occurred independently of the directions communicated by waggle dances associated with past foraging success or the sampling of alternate foraging areas. Migration dance orientation may have been affected by prevailing wind directions, because during the migration period winds blew primarily from the east. However, it is unlikely that wind direction was the only factor influencing migration dance orientation. The lack of immediate flight activity associated with migration dance performance suggests the dances may have gradually prepared colonies for migratory movement by conveying a message to fly for a long, but unspecified distance in a certain direction. Waggle dances associated with migration may therefore function differently from those associated with foraging and nest site selection, which convey both the distance and direction to specific locations.

### **Introduction**

Honey bees, *Apis mellifera*, possess an elaborate system of communication based upon the waggle dance, in which the straight run portion (the waggle-run) communicates the distance and direction to resources (von Frisch, 1967; Winston, 1987; Michelsen et al., 1992). Waggle dance activity provides a powerful tool for investigating collective interactions in honey bees, and has been used to explore spatial colony foraging patterns (Visscher and Seeley, 1982; Schneider, 1989; Schneider and McNally, 1994), colony-level foraging decisions (Seeley, 1986, 1989;

Seeley et al., 1991), and nest cavity selection and route of travel during reproductive swarming (Lindauer, 1955; Seeley, 1985).

The waggle dance may also provide a mechanism for investigating seasonal absconding, or migration, in honey bees. Migration is characteristic of tropical honey bees and (1) consists of an entire colony abandoning a nest site (migration differs from reproductive swarming in that no new queens are produced and the colony does not fission), (2) may occur in response to deteriorating foraging conditions, and (3) may involve travel over great distances (Fletcher, 1978; Winston et al., 1979; Otis et al., 1981; Schneider, 1990; Otis, 1991; McNally and Schneider, 1992; Schneider and McNally, 1992a; 1994). Waggle dances are performed throughout the 1–3 week period in which colonies prepare for seasonal absconding by reducing brood rearing and consuming food stores (Woyke, 1976; Schneider, 1990; Dyer and Seeley, 1991). Dances may also occur on swarm clusters that form at transient stopping points along the migratory pathway (Koeniger and Koeniger, 1980). In migrating colonies of the African race, *A. m. scutellata*, and the Neotropical “Africanized” bee, dances frequently communicate extreme distances (10–20 km) and are performed for a variety of different locations (Schneider, 1990; Ratnieks, 1991). An examination of waggle dances associated with seasonal absconding may therefore provide insights into the regulation and patterns of honey bee migratory movements.

Waggle dances performed during seasonal absconding preparations (preabsconding dances) often occur when there is little or no food collection (Winston et al., 1979; Schneider, 1990). Anecdotal observations suggest that the duration of consecutive waggle-runs performed by individual preabsconding dancers can be highly variable (Ratnieks, 1991; Dyer and Seeley, 1994), such that specific distances may not be communicated. Also, unlike the dances associated with nest site selection during reproductive swarming which become focused on one specific site to which the colony will move (Lindauer, 1955), those preceding migration may not pre-select one particular destination prior to departure (Schneider, 1990). Thus, preabsconding dances may not communicate the location of specific food or nest sites.

Colonies travel in the general direction in which the majority of their preabsconding dances were oriented (Koeniger and Koeniger, 1980; Schneider, 1990; Dyer and Seeley, 1994). These dances may therefore help establish a general route of travel, even if specific destinations are not selected. Dance orientation, and thus the route of colony movement, could be influenced by some assessment of forage availability, or could reflect some abiotic cue such as wind direction. Colonies could orient towards wind-borne, floral odor cues (Fletcher, 1978, 1991), or prevailing winds may indicate weather patterns in distant areas that are conducive to greater resource abundance. However, to date honey bee preabsconding dances have not been quantitatively described, and their communication of specific locations and the factors regulating their orientation have received little systematic investigation.

This study examined the preabsconding dances of the African honey bee, *A. m. scutellata* (hereafter referred to as *scutellata*). The specific objectives were to: (1) determine if the dances communicated particular locations; and (2) examine the factors affecting dance orientation.

## Materials and methods

### *Study Area*

The study was conducted from October 1989 through January 1990 in the Okavango River Delta, Botswana, Africa (19°35.42'S: 23°21.43'E). *A. m. scutellata* colonies in the Okavango are abundant (8/km<sup>2</sup>; Schneider and Blyther, 1988). There is a distinct migration season from November-May that coincides with a period of reduced and variable forage abundance (McNally and Schneider, 1992). Further descriptions of the study area and *scutellata* nesting biology are provided in Schneider and Blyther (1988) and McNally and Schneider (1992).

### *Colony Maintenance*

Waggle dance behavior was investigated using two 2-frame observation colonies (colonies 1 & 2), which provided comb areas similar to the median comb area of naturally occurring nests in the Okavango (Schneider and Blyther, 1988). Each colony was maintained inside a high-walled canvas tent, and each abutted a 2 × 10 cm opening in a tent wall, which allowed free flight to and from the hives. Both observation tents were located in the shade and lined internally with heavy, brown paper. Such modifications reduced the light levels in the tents and minimized the risk of an outside light source altering waggle dance behavior (Schneider, 1989; Schneider and McNally, 1992 a; 1993).

Each colony was initially excavated in the field and the combs and bees were transferred into 45 L hive boxes. Once brood rearing began both colonies were transferred into the observation hives. We began monitoring waggle dance behavior after each colony had inhabited an observation hive for at least seven days. Colonies 1 & 2 were set up in the observation hives in October and November, respectively. Each initiated migration preparations (indicated by the cessation of brood rearing and reduced foraging activity; Schneider and McNally, 1992 a) in December and each migrated from the study area in January. The direction that each colony traveled upon departure was measured using a compass.

### *Monitoring waggle dance activity*

Waggle dance behavior was monitored in both colonies 2–3 days each week of the study period. On each day, the colonies were monitored for 30 min each hour from 0600–1900 hours. Throughout every 30 min period waggle dancers were selected at random, and we determined for each (1) the distance and direction communicated and (2) whether the dancer indicated a food or non-food source. Additionally, we determined (3) flight from the colony during each 30 min period, as an indirect estimate of the recruitment activity associated with the waggle dances. Migrating colonies will sometimes form swarm clusters and perform recruitment dances immediately upon departing from the nest (Schneider, 1990). Thus, when possible we

also monitored waggle dance activity after the colonies had abandoned the observation hives.

In the waggle dance, direction is communicated by the orientation of the waggle-run with respect to vertical. Distance is communicated by waggle-run duration, with more waggle run time corresponding to greater distances (von Frisch, 1967; Winston, 1987). We determined the direction indicated by each dancer by (1) measuring the orientation of the waggle-run with a protractor, and (2) adding the dance angle to the azimuth of the sun calculated for the time of observation using a program for the IBM PC. We determined the distance indicated by each dancer by timing a mean  $\pm$  SD of  $5.9 \pm 4.9$  consecutive waggle-runs, calculating a mean waggle-run duration, and converting this time into a distance estimate in meters. The conversions of waggle-run times into distances was accomplished using a "standard curve", established by training marked foragers from colony 1 to feeding stations at known distances up to 1 km from the hive and then timing their waggle-runs once they returned to the hive (see Schneider, 1990 and Schneider and McNally, 1992a for further descriptions of measuring and translating waggle-run durations). The translation of dance times greater than those covered by the standard curve was accomplished by extrapolation, following the methods of Dyer and Seeley (1991). The distance-dance time relationships for different *scutellata* colonies in the Okavango are similar (Schneider, 1989) and thus we used the curve for colony 1 to estimate foraging distances for both observation colonies. At present, we do not know if our standard curve based upon 1 km accurately estimated the extreme distances communicated by preabsconding dancers. However, the present study was primarily concerned with comparing the behavior and precision of distance communication by nonabsconding and preabsconding dancers (see below), and not with the absolute distances indicated. Thus, possible errors in our distance estimates should not have affected the general conclusions of the study.

A dancer was considered to be associated with a food source if it carried pollen loads or offered samples of nectar to followers during dance performance. Dancers not carrying pollen or not offering nectar samples were considered to be associated with non-food sites.

Flight activity was estimated during each 30-min period by conducting five 1-min counts, each separated by at least 5 min, of the numbers of bees flying from the hive. A mean number of flights/min was subsequently calculated for each observation period.

#### *Determining the association of waggle dances with specific sites*

The communication of specific sites was investigated by comparing two categories of waggle dancers: (1) nonabsconding dancers (those communicating distances less than 4 km during the period preceding seasonal absconding preparations); and (2) preabsconding dancers (those communicating distances greater than 4 km during the period that occurred between the onset of absconding preparations and colony departure). During nonmigratory periods, *scutellata* colonies concentrate 90–95% of all foraging activity within 3–4 km of the hive (Schneider, 1989; Schneider and

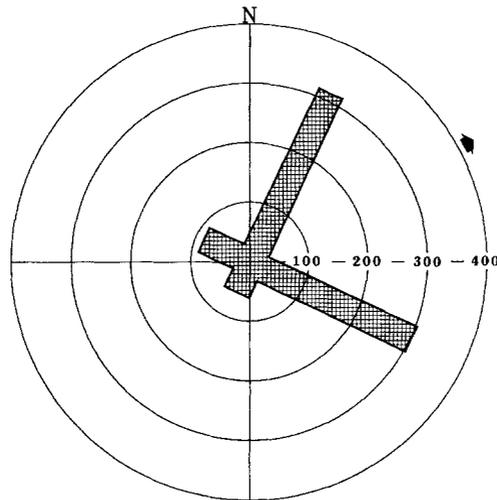
McNally, 1992a; 1993). Thus, the nonabsconding dancers represented the more typical dance behavior of Okavango bees, while the preabsconding dances may have been associated with regions far removed from the regular foraging range. For each colony we randomly selected 75 dancers (3–4/day of observation) for the nonabsconding category, to make sample sizes between the two dancer groups more equal.

Three aspects of waggle dance behavior were compared between the two categories of dancers: (1) the number of dancers associated with food sources; (2) the flight activity associated with dance performance; and (3) the variability in the distances communicated by consecutive waggle-runs of individual dancers. Intraindividual variability in distance communication was examined by calculating the SD for the duration of the consecutive waggle-runs measured for each bee, and then expressing this value as a coefficient of variation (CV). The CVs of the two dancer categories were subsequently compared using Analysis of Variance and Student-t tests.

#### *Determining the factors affecting preabsconding dance orientation*

We examined three factors that may have influenced the directions indicated by preabsconding dances: (1) the sampling of sites outside the regular foraging range; (2) foraging success within the regular foraging area prior to the onset of migration preparations; and (3) wind direction. Dancers were considered to be sampling from remote sites if they communicated distances greater than 4 km during the nonabsconding period. We compared the number of “sampling” dancers and preabsconding dancers in each colony that indicated sites located North (315–44°), East (45–134°), South (135–224°) and West (225–314°) of the hive. We also determined the number of dancers in each colony that indicated food sites located North, East, South and West within a 4 km radius of the hive (the regular foraging range) during the 2 week period preceding migration preparations. Chi Square analysis was used to compare the number of foraging and preabsconding dancers associated with each compass quadrant.

Wind direction data collected at a standard height using recognized techniques were not available for the study site. As far as can be determined, the only wind data available for the Okavango Delta are those collected by the U. S. Air Force during a nine year study (1956–1964) in the village of Maun, located approximately 50 km south of the study area (USAF ETAC 1970). The age of these data, plus their collection at a different site, made comparisons between wind directions and preabsconding dance orientations potentially suspect. However, the USAF data revealed that 84% of all measurements (N = 733) taken during December and January (the months preceding and coinciding with the observation of preabsconding dances in the present study) indicated winds blowing from the N-NE and E-SE (Fig. 1). Observations of wind direction made with a compass at ground level during December and January in the present study revealed that 76% of all measurements (N = 544) were for N-NE and E-SE winds. While we were unable to conduct above-ground wind measurements, this comparison suggests that general wind patterns during the study period were similar to those recorded in 1956–1964, and we therefore felt justified in using the older wind data.



**Figure 1.** The number of wind measurements oriented N-NE, E-SE, S-SW and W-NW during December and January. The bars are centered about the midpoint for each compass quadrant; the arrow indicates the mean wind angle. Data were taken from a 9 year study (1956–1964) conducted approximately 50 km south of the study area (USAF ETAC, 1970). Measurements taken at ground level during the study period revealed similar patterns for wind direction at the study site

Two approaches were utilized to assess the relationship between wind direction and preabsconding dance orientation. First, we used statistical methods for circular distributions to calculate the mean angle of orientation for wind direction and the preabsconding dances in each colony (Zar, 1974). The mean angles were then compared using the Watson-Williams test (Zar, 1974). This first approach provided a more fine-grained examination of the association between wind direction and preabsconding dance performance. However, wind directions during December and January were highly variable. While the vast majority of measurements during these months indicated winds blowing from a generally easterly direction, 43 % were from the N-NE and 41 % from the E-SE (the remaining 16 % of wind measurements were from a westerly direction; Fig. 1). We therefore utilized a second, more coarse-grained approach in which we compared the observed number of preabsconding dances in each colony oriented towards an easterly (N-NE and E-SE) versus a westerly (S-SW and W-NW) direction to that expected based on the overall proportions of easterly versus westerly winds.

Migrating *scutellata* colonies in the Okavango exhibit seasonal changes in the directionality of movement. Colonies emigrate in an easterly direction during the migration season (November–May), but travel in a westerly direction to move back into the study area in June–August when floral resources are most abundant (McNally and Schneider, 1992). We therefore further examined the relationship between wind direction and colony movements by determining if winds shifted seasonally in a way that could influence such reversals in the direction of travel.

Unless otherwise stated all mean values are reported as  $\pm$  one SD. The CVs for waggle-run durations were log transformed prior to analysis to ensure homogeneity of variances among the two categories of dancers.

## Results

Colonies 1 & 2 were monitored on a total of 36 and 35 days, respectively, over a three month period. For colony 1, 27 days of observation occurred during the non-migration period, while the remaining 9 days occurred after migration preparations had been initiated. These values for colony 2 were 25 and 10 days, respectively. A total of 2874 waggle dancers were monitored in colony 1, of which 2799 were observed during the nonabsconding period and 75 were preabsconding dancers. In colony 2, 2227 dancers were monitored, 2207 of which occurred prior to absconding preparations and 20 were preabsconding dancers. Neither colony formed a swarm cluster and performed recruitment dances immediately upon abandoning the nest. Thus, all preabsconding dances were observed within the observation hives during the 2–3 week period between the onset of migration preparations and emigration. The mean distances communicated over all nonabsconding dancers in colonies 1 & 2 were  $399.7 \pm 252.5$  m and  $472.8 \pm 353.4$  m, respectively. The mean distance communicated by preabsconding dancers in colony 1 was  $7238 \pm 3908$  m (range = 4033–23,197 m) and in colony 2 was  $6254 \pm 3686$  m (range = 4012–19,516 m).

### *Association of preabsconding dances with specific sites*

Compared to nonabsconding dancers, preabsconding dancers were less associated with food sites and flight from the nest, and exhibited greater intraindividual variability in the communication of distance. In both colonies only 5–7% of the preabsconding dancers observed engaged in trophallaxis with followers, and none carried pollen (Tab. 1). In contrast, 71–87% of all nonabsconding dancers observed engaged in trophallaxis or carried pollen loads while dancing (for both colonies Chi Sq.  $> 50.0$ ; d.f. = 2;  $P < 0.001$ ).

Flight activity during periods of preabsconding dance performance was 6–20 times less than that observed in association with nonabsconding dances (Tab. 1). It was not possible to directly compare the means for flight activity among the two dance groups, because of the large number of zero values for the preabsconding dancers (71% of pre-absconding dancers in colony 1 and 40% in colony 2 were observed during periods of no flight activity). Thus, we assigned a colony flight activity value to each dancer based on the following scale: 0 = 0–1 flights from the hive/min; 1 = 2–20 flights/min; 2 =  $> 20$  flights/min. Subsequent Chi Square analysis revealed significantly less flight activity associated with preabsconding dance versus nonabsconding dance performance in both colony 1 (Chi Sq. = 86.9; d.f. = 2;  $P < 0.001$ ) and colony 2 (Chi Sq. = 11.4; d.f. = 2;  $P < 0.01$ ). The low flight activity suggested that there was little or no immediate recruitment of followers associated with preabsconding dance performance.

**Table 1.** Characteristics of the waggle-runs performed by nonabsconding and preabsconding dancers in Colonies 1 and 2. The number of nonmigration dancers was restricted to 75 for each colony to make sample sizes between the two categories more similar. CV represents the coefficient of variation for the duration of consecutive waggle-runs by individual bees. Number of flights from the hive/min refers to the flight activity observed during the 30 min periods in which waggle dancers were monitored. All mean values are reported as  $\pm$  one SE

	N	Waggle-run Duration (s)	CV	No. Associated with Food Source	No. flights from hive per min
<i>Colony 1</i>					
Nonabsconding	75	1.72 $\pm$ 0.19	0.065 $\pm$ 0.003	53	13.29 $\pm$ 1.70
Preabsconding	75	17.12 $\pm$ 1.04	0.244 $\pm$ 0.002	5	0.55 $\pm$ 0.21
<i>Colony 2</i>					
Nonabsconding	75	1.34 $\pm$ 0.14	0.073 $\pm$ 0.004	65	12.45 $\pm$ 1.57
Preabsconding	20	14.86 $\pm$ 1.89	0.202 $\pm$ 0.021	1	2.14 $\pm$ 0.51

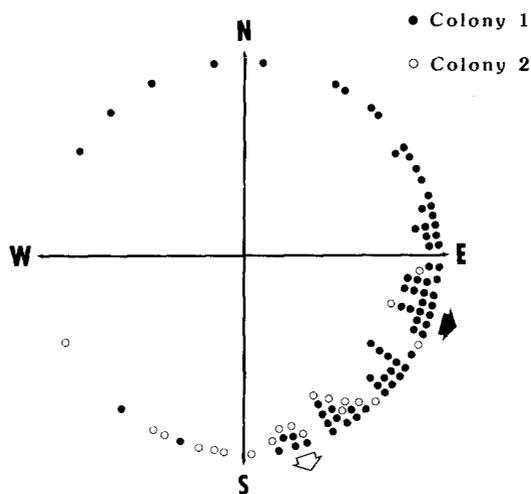
The mean CVs for waggle-run duration for the preabsconding dancers were approximately 3–4 times greater than those observed for nonabsconding dancers [Tab. 1;  $t = 14.2$ ; d. f. = 243;  $P < 0.001$ ; mean CVs for colonies 1 & 2 did not differ within either the preabsconding or nonabsconding categories (for both comparisons  $P > 0.05$ ), and thus the data were combined within categories]. Eighty-five percent of all preabsconding dancers communicated distances that varied by at least 1000 m in consecutive waggle-runs; 13% had consecutive indications of distance that varied by 5–10 km. Thus, compared to the distances indicated by nonabsconding dancers those of preabsconding dancers were much less precise, suggesting that specific distances (and by inference specific sites) were not communicated.

#### *The factors influencing preabsconding dance orientation*

The directions indicated by the preabsconding dancers in colonies 1 & 2 are depicted in Fig. 2. Those observed for colony 1 were mostly in the NE to S (8, 49, 17 and 1 dances were oriented N, E, S and W, respectively). Those of colony 2 were concentrated primarily in the S-SE quadrant (0, 3, 16, and 1 oriented N, E, S and W).

Waggle dances for sites located outside the regular foraging range were observed only rarely, and such sampling of distant areas did not appear to influence preabsconding dance orientation. Of the 11 and 9 sampling dances observed in colonies 1 & 2, respectively, most were oriented towards the N or W (6, 0, 1 and 4 dances in colony 1 were oriented N, E, S and W; these values for colony 2 were 6, 1, 2 and 0 dances). Because of the small number of sampling dances observed, we used a proportions test (Zar, 1974) to compare the proportions of preabsconding and sampling dances oriented in a general easterly versus westerly direction. In both colonies the distribution of preabsconding dances among the compass quadrants differed significantly from that of the sampling dances ( $P < 0.01$  for each colony).

Preabsconding dance orientation also was not influenced by the directions communicated by successful foragers for sites within the regular foraging range prior



**Figure 2.** The direction communicated by each migration dancer in colonies 1 & 2. The closed arrow indicates the mean dance angle for colony 1; the open arrow indicates the mean angle for colony 2. The distances communicated by the dancers are not indicated. Both colonies traveled in a direction between  $110^{\circ}$ – $130^{\circ}$  upon departure

to emigration. During the final two weeks preceding absconding preparations, the majority of foraging dances in both colonies were oriented towards the N and W (for colony 1: 529 foraging dances observed; 147, 133, 31 and 222 oriented N, E, S and W; for colony 2: 357 foraging dances observed; 212, 30, 13 and 102 oriented N, E, S and W). The distribution of preabsconding dances among the four compass quadrants differed significantly from that of the foraging dances (for each colony, Chi Sq.  $> 120.0$ ; d. f. = 3;  $P < 0.001$ ).

There may have been an association between prevailing easterly wind directions and preabsconding dance orientation, although such an association was not well defined. The mean angles of orientation for preabsconding dances in colonies 1 & 2 ( $108^{\circ}$  and  $163^{\circ}$ , respectively; Fig. 2) differed significantly from the mean wind angle of  $60^{\circ}$  (Fig. 1; for both comparisons,  $F > 50.0$ ;  $P < 0.01$ ). However, there was considerable variability in preabsconding dance and wind orientations (angular deviations for colonies 1 & 2 and wind =  $47.7^{\circ}$ ,  $34.9^{\circ}$ , and  $68.7^{\circ}$ , respectively), such that there was broad overlap of dance and prevailing wind directions. Indeed, there was no significant difference in the observed number of preabsconding dances oriented in an easterly versus a westerly direction and that expected based upon the prevailing easterly winds in either colony 1 (Chi square = 3.27,  $P > 0.05$ ; Figs. 1 & 2 or colony 2 (proportions test;  $Z = 1.02$ ;  $P > 0.05$ ). Upon departure from the study area both colonies headed between  $110^{\circ}$ – $130^{\circ}$  SE. Thus, preabsconding dance orientation, and perhaps the route of colony travel, may have been affected by the prevailing winds that occurred prior to emigration.

However, we found no seasonal shifts in wind patterns that corresponded to changes in the directionality of *scutellata* colony movements. During June–August, when there is a large influx of colonies into the study area traveling in a westerly

direction (McNally and Schneider, 1992), winds continue to blow predominantly from the east (USAF ETAC 1970).

## Discussion

The preabsconding dances of *A. m. scutellata* communicated distances much greater than those traveled during normal foraging, but were not associated with food sources and occurred during periods in which flight activity was reduced or absent. Furthermore, the distances indicated by consecutive waggle-runs of individual bees could vary by as much as 1–10 km. Thus, it seems unlikely that preabsconding dances communicated the location of, or stimulated immediate recruitment for, specific, distant foraging or nesting sites. Because upon departure colonies traveled in the general direction in which their preabsconding dances were concentrated, our results support the suggestion by Schneider (1990) that these dances function to establish a general direction of colony travel, but not a particular destination. Preabsconding dances in the tropical honey bee, *A. dorsata*, also communicate distances greater than those associated with foraging, exhibit considerable intra-individual variability in waggle-run duration, may occur when flight activity is reduced, and are concentrated in the direction of colony movement (Koeniger and Koeniger, 1980; Dyer and Seeley, 1993). Thus, waggle dances that determine a direction of colony travel without establishing specific destinations may be characteristic of tropical honey bees that undergo seasonal migratory movements. Because such dances occur only in association with seasonal absconding, we propose they be referred to as “migration dances”.

The factors influencing the directions indicated by migration dances in *scutellata* are unclear at present. Migration dance orientation was not influenced by the orientation of either sampling dances or dances for food sites within the regular foraging range. In both colonies examined sampling and foraging dances were orientated primarily towards the N and W, while migration dances were oriented E and S. These observations suggest that migration dance orientation and the route of colony travel can occur independently of waggle dances associated with past foraging success or alternate, distant foraging areas. However, our results do not exclude the possibility that scouts sampled sites in the direction of migratory movement without performing dances, and that such sampling activity may have affected the route of colony travel.

Our results on the relationship between colony migratory movements and wind direction are equivocal. The majority of migration dances observed in this study were oriented E-SE. The prevailing wind direction during the migration period in the Okavango is also easterly, and E-SE was the general direction of travel for migrating colonies in the present and previous studies (see also McNally and Schneider, 1992). However, there are no seasonal shifts in wind direction that correspond to the westerly direction of travel for colonies that move into the study area in June–August. Thus, the observed relationship between preabsconding dance orientation and the prevailing easterly wind direction in the present study may have been coincidental. Alternatively, wind patterns may influence migration dance orientation

and colony travel during certain portions of the absconding process, but may not be the only factor affecting the direction of movement throughout all phases of *scutellata* migration.

The characteristics observed for migration dances in this study may have reflected the dynamics of the emigration process in *scutellata*. While colonies can forage throughout much of the year (Schneider and McNally, 1992 b), local availability of resources may be unpredictable due to the unpredictable rainfall patterns of southern Africa (Griffiths, 1976; Sinclair, 1983; Rinderer, 1988). Migration may therefore have to occur over long distances to follow shifting resource patterns (Fletcher, 1978; Schneider and McNally, 1992 a). During such movements, colonies may periodically stop and forage from swarm clusters to replenish food stores and assess the quality of an area (Otis et al., 1981; Otis, 1991; Koeniger and Koeniger, 1980; Dyer and Seeley, 1993). If combs are unlikely to be constructed at the transient stopping points then the preselection of, and recruitment for, specific sites prior to departure may be unnecessary. Rather, it may be more important to establish a general route of travel that will potentially result in movement into an area of better resource conditions. If during some parts of the migration process colonies are unable to determine the direction of travel using an assessment of resource availability, then wind direction may provide an alternate orientation cue. Prevailing winds may convey floral odors over long distances (Fletcher, 1978, 1991), or may reflect weather patterns in remote regions that are associated with increased forage abundance.

Taken together, our results suggest that waggle dances associated with migration function differently from those involved in foraging and nest site selection in two main respects. First, migration dances convey less specific information. During foraging and nest site selection, nestmates must be accurately recruited to a particular location and dances provide specific information about direction and distance (von Frisch, 1967). In contrast, during migration colonies may have to travel unknown distances, and dances may communicate only a direction of movement. Thus, honey bees may modify the information content of waggle dances when used in different contexts.

Second, migration dances may elicit responses that operate on a different time scale. The low levels of flight often associated with migration dances suggest there is little or no immediate impact upon recruitment. Migration dances may therefore exert a more delayed effect, which gradually prepares colonies for long-distance flight. Responses to the honey bee waggle dance may therefore occur on two time scales: (1) short-term, in which workers are recruited more-or-less immediately to specific food and nest sites; and (2) long-term, in which colonies are readied for migratory travel. Other communicatory signals of honey bees may also influence behavior on more than one time scale. For example, the vibration dance, which causes increased activity that enhances foraging-age bees contacting recruiting stimuli, may help adjust food collection to both short-term fluctuations in floral availability as well as more long-term trends in resource abundance (Schneider et al., 1986 a, b; Schneider, 1987; Schneider and McNally, 1991).

Thus, migration dances in tropical honey bee colonies may be an integral part of the emigration process. The characteristics of migration dances suggest that the waggle dance may convey somewhat different messages, depending upon the

precision required in the communication of distance and the time course of response by followers in different situations. Waggle dances may therefore exert more than one effect on colony activity.

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