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Original article

"Migration dances" in swarming colonies of the honey bee, *Apis mellifera**

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Abstract – The migration dance is a type of dance behavior typically found in tropical honey bee colonies that are preparing for seasonal absconding. Here we report the occurrence of migration-like dances in colonies of European honey bees, *Apis mellifera*, preparing for reproductive swarming. Compared to waggle dances performed during the same periods, the migration dances lacked the "figure-8" pattern of performance, could be performed when there was no flight from the hive, did not necessarily stimulate immediate recruitment, communicated extreme but highly variable distances, and did not communicate consistent directions of travel. Because the dance occurs when colonies are preparing for both seasonal absconding and swarming, we proposed that it be called the "relocation dance". The possible functions of relocation dances during preparations for reproductive swarming are discussed.

migration dance / waggle dance / swarming / absconding / seasonal migration

1. INTRODUCTION

Honey bees exhibit two types of colony movement: swarming and absconding. Swarming is the method of colony reproduction and involves about half the workers and the laying queen moving to a new nest site, while the remaining bees stay in the original nest and finish rearing replacement queens. Reproductive swarming involves a 2–4 week preparation period in which new queens are produced and the laying queen is prepared to leave the nest (Winston, 1987; Pierce et al., 2007). In contrast, absconding is not a reproductive process and does not involve colony fission or the raising of new queens. Rather, it consists of an entire colony abandoning a nest and relocating to a new site (Winston, 1987; Oldroyd and Wongsiri, 2006). Absconding can occur in response to disturbances to the nest (disturbance-induced absconding) or a deteriorating foraging environment (seasonal absconding or migration). Seasonal absconding is characteristic of tropical races of honey bees (it is never observed in temperate-climate races) and can involve migratory movements of up to 100 km to follow shifting resource patterns (Seeley, 1985; Schneider and McNally, 1992; Oldroyd and Wongsiri, 2006). Although disturbance-induced absconding can occur relatively quickly, seasonal absconding involves 2–4 weeks of preparation, during which foraging virtually ceases, young larvae are cannibalized, and food stores are consumed. Departure occurs after the last brood has emerged, such that a colony leaves behind only empty combs (Schneider and McNally, 1992; Oldroyd and Wongsiri, 2006).

Colony movements in honey bees involve two types of dance behavior: waggle dances and migration dances (also called migratory dances or absconding dances; Koeniger and Koeniger, 1980; Sasaki, 1990; Dyer, 2002). Waggle dances are performed on both reproductive and absconding swarm clusters to communicate the distance and direction to

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potential nest cavities, and are used to select a specific destination during the house-hunting process (Seeley and Buhrman, 1999; Camazine et al., 1999). In contrast, migration dances are performed in the nest throughout the 2–4 weeks preceding seasonal absconding, and may also occur on swarm clusters that form at intermediate stopping points during the journey (it is unknown if migration dances occur during disturbance-induced absconding; Ratnieks, 1991; Schneider and McNally, 1992; Oldroyd and Wongsiri, 2006). Migration dances are not associated with nest-site selection, but may help determine a general route of colony travel (Dyer, 2002).

Migration dances differ from waggle dances in five main ways. First, and most noticeably, they lack the "figure-8" pattern of waggle dances. After a migration dancer completes a waggle run, she does not circle back around to her starting point, but rather walks forward on the combs before repeating the waggle run (Koeniger and Koeniger, 1980; Sasaki, 1990; Schneider and McNally, 1994). As a result, unlike waggle dances which occur in localized areas of the colony, migration dances are performed while roaming throughout large regions of the nest. Second, migration dancers produce inconsistent lateral movements of the body during the waggle run. Whereas waggle dancers show a fairly constant rate of side-to-side motion during a waggle run, migration dancers change the rate of waggling within a single waggle run, resulting in a halting or "sputtering" appearance. Third, migration dances communicate extreme distances, ranging up to 25–35 km (Sasaki, 1990; Dyer and Seeley, 1994; Schneider and McNally, 1994). In contrast, waggle dances for nest sites typically indicate distances within 1–5 km of the natal nest (Lindauer, 1955; Schneider, 1995; Camazine et al., 1999). Fourth, it is unlikely that migration dancers communicate the location of specific sites. The indication of distance by individual migration dancers is highly inconsistent and consecutive waggle runs by the same bee can communicate distances that vary by as much as 5–10 km (Dyer and Seeley, 1994; Schneider and McNally, 1994). However, migration dances tend to communicate a consistent direction and are often oriented in the general direction that an absconding colony will eventually travel (Schneider, 1990; Schneider and McNally, 1994; Dyer, 2002). Thus, migration dances probably do not indicate particular destinations, but may help to establish a direction of travel. Finally, migration dances often occur when there is little or no flight from the nest, which suggests that they do not stimulate immediate recruitment (Dyer and Seeley, 1994; Schneider and McNally, 1994). Thus, unlike waggle dances, which recruit followers to specific foraging and nest sites, migration dances may help to prepare colonies for seasonal absconding by conveying the message to fly for long, but unspecified distances in a certain direction (Schneider and McNally, 1994; Dyer, 2002).

Migration dances have been reported for the African honey bee subspecies, *A. m. scutellata* (Schneider, 1990; Schneider and McNally, 1994), the Asian honey bee, *A. cerana japonica* (Sasaki, 1990), and the giant tropical honey bee, *A. dorsata* (Koeniger and Koeniger, 1980; Dyer and Seeley, 1994; Oldroyd and Wongsiri, 2006). Indeed, migration dances are considered to be unique to tropical honey bees that undergo seasonal migratory movements (Schneider and McNally, 1994; Oldroyd and Wongsiri, 2006). However, while conducting studies of reproductive swarming in European honey bee colonies, we observed dance behavior that exhibited the characteristics of migration dances. Here we characterize these dances and examine their possible role in the swarming process. Our specific objectives were to describe the frequency of occurrence of migration-like dances during swarming preparations, determine the age of the dancers and their behavior within the nest, and compare the distances and directions communicated by migration dances with those communicated by waggle dancers for food and nest sites.

2. MATERIALS AND METHODS

2.1. Study colonies

We investigated dance behavior in four European honey bee colonies (A, B, C and D) on the

campus of the University of North Carolina at Charlotte in 1998 and 1999. The colonies were maintained in four-frame observation hives and allowed to develop and swarm naturally. Each contained a population of known-age bees established by adding 300–500 newly emerged, paint-marked workers every other day over a 4–7 week period preceding swarming. The marked populations were created as part of a larger study of swarming behavior and details of their establishment are given in Lewis and Schneider (2000).

2.2. Monitoring dance behavior

Observations were initiated when the colonies became crowded, and were then continued for 4–6 weeks until swarm departure. Each colony was monitored for 30-min periods 5–10 times/d for at least four days each week until swarming occurred. During each 30-min period, we recorded every occurrence of workers performing migration-like dances. A worker was identified as a possible migration dancer if her dances lacked a figure-8 pattern and she exhibited an inconsistent rate of waggling during a waggle run. To more fully determine that the putative migration dances differed from waggle dances for food and nest sites, we also recorded the behavior of randomly selected, typical waggle dancers that were observed during the same 30-min periods in which migration dancers were monitored.

For each migration dance and waggle dance monitored, we recorded the time of day of performance and the age of the dancer, if she was a paint-marked bee. We compared the ages of migration and waggle dancers using a two-way ANOVA with dance type (migration or waggle) and colony as independent variables.

We also estimated the distance and direction communicated by each dancer. Distance was estimated by using digital stopwatches to record the duration (in seconds) of 8.9 ± 0.9 (mean ± SE) consecutive waggle runs, then calculating a mean waggle-run time. The mean waggle-run times were converted into a distance estimate (m) using the regression formula: *distance* = 1339.882 (*waggle-run time*) −773.69, which was generated from data presented by von Frisch (1967; Tab. 13) for waggle-run durations for distances $\geq$ 500 m (r^2 = 0.999).

We estimated the variability in each dancer's indication of distance by calculating the coefficient of variation (CV), in which the standard deviation for the duration of consecutive waggle runs was expressed as a percentage of the mean. We then compared the waggle-run durations and CVs of migration dances and waggle dances within and between colonies using two-way ANOVAs with dance type and colony as independent variables. Prior to analysis, we corrected the coefficients of variation for bias (Sokal and Rohlf, 1995) and log transformed the unbiased CVs to achieve normality. For our statistical analyses of waggle-run durations and CVs, we used only data from bees with characteristic paint marks or other distinguishing features that allowed for individual recognition, to prevent including an individual bee more than once. All mean values are reported as ± one SE.

The direction communicated by each dancer was estimated by measuring the orientation of its waggle run with respect to vertical using a protractor. We then added the dance angle to the sun's azimuth at the time of observation using the program available at http://aa.usno.navy.mil/data/docs/AltAz.html. We used statistics for circular distributions (Zar, 2007) to examine the indicated directions. We first calculated for the migration and waggle dancers in each colony the mean angle communicated and the angular deviation. To examine if migration dancers were focused on a particular direction, we used the Rayleigh's test (Zar, 2007) to determine if the pattern of dance angles within each colony differed from a random distribution. We used the Watson-Williams test (Zar, 2007) to compare the dance angles communicated by migration and waggle dancers within each colony. The sequential Bonferroni adjustment was used to determine significance levels for the Rayleigh's and Watson-Williams tests.

After each colony swarmed, we captured the cluster and transferred it to an observation stand, following the methods of Lewis and Schneider (2000) and Pierce et al. (2007). Each swarm was fed a sucrose solution (50% by volume) ad libitum while on the swarm stand to minimize dancing for food sites and ensure that the vast majority of waggle dances communicated the location of nest sites. Each swarm was monitored continuously and every bee observed to perform waggle dances or migration dances was marked with a distinguishing dot of paint. When monitoring the swarms, we recorded only the number of the different dancer types; we did not record the distances and directions communicated.

Table I. Age of dancers and the characteristics of the waggle runs performed by migration dancers and waggle dancers in each of the four swarming colonies examined. Sample sizes indicate the total number of dancers monitored, both marked and unmarked; statistical analyses were restricted to those dancers that were individually distinguishable. No waggle dancers were observed on the days of migration dance performance in Colony D, and none of the migration dancers were of known age. Mean values are reported as ± one SE.

Dancers	Age (days)	Waggle-run Duration (s)	Distance Communicated (m)
Colony A			
Migration (n = 4)	19.5 ± 0.5	7.74 ± 1.40	9600 ± 1885
Waggle (n = 6)	18.8 ± 0.7	2.77 ± 0.41	2938 ± 544
Colony B			
Migration (n = 6)	23.1 ± 0.4	11.29 ± 1.25	14 399 ± 1678
Waggle (n = 8)	21.6 ± 2.8	3.32 ± 0.96	3677 ± 1291
Colony C			
Migration (n = 8)	20.0 ± 1.1	10.70 ± 0.76	13 585 ± 1017
Waggle (n = 17)	22.2 ± 1.5	3.02 ± 0.47	3264 ± 631
Colony D			
Migration (n = 7)	—-	10.20 ± 1.75	12 889 ± 2347

3. RESULTS

3.1. Frequency and patterns of migration dance performance

Migration-like dances occurred in all four observation colonies, but only during the two weeks immediately preceding swarming. During these periods, we monitored a total of 25 migration dancers (Tab. I), 15 of which (3.8 ± 0.5/colony) were individually distinguishable. We monitored a total of 31 waggle dancers during the same periods (Tab. I), 20 of which (5.1 ± 2.0/colony) were individually recognizable. The mean age of the two dancer types did not differ ($F_{1,26}$ = 0.20; P = 0.565) and this trend was similar among colonies ($F_{2,26}$ = 0.19; P = 0.831).

Migration dances were observed throughout the day and most occurred during periods of strong flight activity. However, migration dances could also occur when there was little or no flight from the colonies. For example, all migration dances observed in colony D occurred between 0730 and 0900 h on two separate days of cool rainy weather, during which there was no flight from the hive and no waggle dances were observed (Tab. I). In contrast, all waggle dances monitored occurred during periods of intense flight activity from the observation hives.

Migration dancers typically danced for extended periods of time while roaming over all combs in the colony. They often performed waggle runs continuously throughout a 30-min observation period without leaving the hive, and two of the marked migration dancers danced continuously during 2–3 consecutive 30-min periods. Workers attended to the migration dances throughout the period of performance, although we did not determine the amount of time individual bees followed the dancers. In comparison, waggle dancers typically danced for less than 5 min before leaving the hive and largely confined their activity to the lower comb of the nest.

3.2. Distance and direction communicated by migration and waggle dancers

The mean duration of waggle runs for bees identified as possible migration dancers (10.42 ± 1.13 s) was almost four times longer than the 2.88 ± 0.32 s observed for waggle dancers ($F_{1,28}$ = 39.12; P < 0.0001). There was no dance type by colony interaction ($F_{3,28}$ = 1.24; P = 0.304; Tab. I), indicating that the differences in dance times were similar among colonies. The mean waggle-run durations corresponded to distances of 13 197 ± 867 m and 3083 ± 430 m, respectively (Tab. I). Eight of the migration dancers communicated distances greater than 16 km and two indicated distances of 22–29 km.

Compared to waggle dances, migration dances exhibited much greater variability (and by inference, much less precision) in the

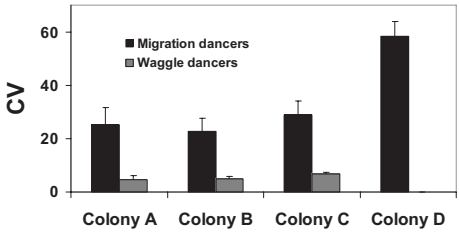

Figure 1. Mean ± SE Coefficients of Variation for the duration of consecutive waggle runs performed by individual migration and waggle dancers in the study colonies. Migration dances in colony D were observed during two days of cold rainy weather, during which there was no waggle dance activity.

distances communicated by the consecutive waggle runs performed by the same bee. The mean CV for the waggle-run durations of migration dances (31.9 ± 4.38) was five times greater than the 5.74 ± 0.59 calculated for the waggle dancers ($F_{1,28}$ = 70.11; P < 0.0001; Fig. 1), and this trend was exhibited similarly among colonies ($F_{3,28}$ = 0.23; P = 0.794). All of the migration dancers communicated distances in consecutive waggle runs that varied by at least 2800 m. Furthermore, 66% had consecutive indications of distance that varied by 5–15 km, and 12.5% communicated distances that varied by 20–36 km. In contrast, the consecutive indications of distance by the waggle dancers varied at most by only 60–300 m.

The degree to which migration dances were focused on particular directions varied among colonies. The directions communicated by migration dancers were randomly distributed in colony A (Rayleigh's Test: R = 2.89; P > 0.05) and colony B (R = 1.94; P > 0.05) (Fig. 2). In contrast, the dance angles for migration dances differed from a random distribution in colony C (R = 8.66; P < 0.05) and colony D (R = 5.98; P < 0.05) (Fig. 2). However, the distribution of directions indicated by migration dancers was similar to that of waggle dancers in colony A (Watson-Wilson test: $F_{1,9}$ = 3.85; P > 0.05), colony B ($F_{1,16}$ = 4.40; P > 0.05), and colony C ($F_{1,23}$ = 7.56; P > 0.05 at adjusted alpha level) (Fig. 2; no waggle dances were observed in colony D on the days migration dances were monitored). Thus, migration dances did not consistently indicate particular directions and the directions communicated were as variable as those indicated for scattered food sites.

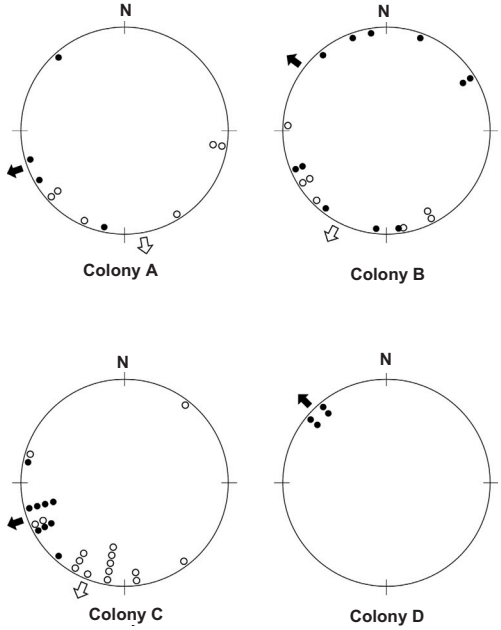

Figure 2. The directions communicated by the individual migration dancers (closed circles) and waggle dancers (open circles) in each of the four swarming colonies monitored. Closed arrows indicate the mean directions communicated by migration dancers; open arrows indicate the mean directions communicated by waggle dancers. No waggle dancers were observed in colony D during the periods in which migration dances occurred.

3.3. Migration dances performed on swarm clusters

Migration dancers were observed on three of the four swarm clusters, although their occurrence was rare. We observed one migration dancer on the swarm that issued from colony A, two on the swarm from colony B, and one on swarm D. In contrast, we observed 442 ± 72 different nest-site dancers on each swarm.

4. DISCUSSION

We observed dances exhibiting the features of migration dances during preparations for reproductive swarming in all four of

the colonies monitored. The dances were never observed earlier than two weeks before swarming, even though each colony was monitored for 4–7 weeks before swarm departure. Furthermore, over the years we have monitored many other observation colonies that were not preparing for reproductive swarming, and migration dances have never been observed. In combination, these observations suggest that the migration-like dances we describe here occur only during the swarming-preparation period. Although the occurrence of migration dances in swarming colonies has been previously suggested (Schneider and Lewis, 2003), our study is the first to characterize these dances for European honey bees, and for any honey bee race in association with reproductive swarming.

The migration dances differed from waggle dances observed during the swarming periods and exhibited many of the same characteristics previously described for tropical honey bees undergoing seasonal absconding: (1) they lacked the typical figure-8 pattern of waggle dances, (2) they were performed for extended periods of time throughout large areas of the nest, (3) they could occur when there was little or no flight from the colonies, and (4) they communicated extreme but highly variable distances (Sasaki, 1990; Schneider and McNally, 1994; Dyer and Seeley, 1994). This type of dance behavior is therefore not restricted to seasonal absconding in tropical honey bees. Both reproductive swarming and seasonal, migratory absconding involve long-term preparations to ready a colony for relocating to a new site (Schneider, 1990; Oldroyd and Wongsiri, 2006; Pierce et al., 2007). Because migration-like dances can occur during the preparation periods for both types of colony movement, we propose that the dances be referred to as "relocation dances".

The number of relocation dancers observed in the present study (4–8 per colony) was quite low, and considerably less than the 20–75 migration dancers reported for colonies of *A. m. scutellata* preparing for seasonal absconding (Schneider and McNally, 1994). We do not know what effect (if any) this small number of dancers may have on the swarming process. However, relocation dancers performed the signal for extended periods throughout the nest and were potentially contacted by large proportions of the worker population. This, in turn, could have influenced swarming preparations in our European colonies in at least two ways.

First, the dances could have helped to determine a route of travel. Schneider and McNally (1994) observed that during seasonal absconding in *A. m. scutellata*, migration dances were oriented in the direction that a colony flew after it abandoned the nest. We did not determine the direction of travel for our swarms and thus we can not fully evaluate this possible function. However, relocation dances were not consistently focused on particular directions in all swarming colonies, and the directions indicated were as variable as those communicated for food sites. Furthermore, reproductive swarms initially cluster in vegetation near the original colony and then travel only a few kilometers to a pre-selected nest site, the location of which is communicated by waggle dances (Schneider, 1995; Camazine et al., 1999; Visscher, 2007). It seems unlikely that swarms would need an additional dance behavior to establish a direction of movement to either the initial clustering site or the new nest site. Thus, while relocation dances may help determine a route of travel during seasonal migratory movements, it is questionable whether they play the same role during reproductive swarming in *Apis mellifera*.

Second, relocation dances may help to prepare workers to abandon the natal nest. Three lines of evidence are consistent with this hypothesis. First, it is unlikely that relocation dancers communicate specific sites to which a swarm will move. The distances indicated by relocation dancers are well beyond those normally traveled by reproductive swarms (Lindauer, 1955; Schneider, 1995; Camazine et al., 1999) and the consecutive waggle runs by individual dancers communicate highly variable distances. Second, relocation dances may not always generate immediate recruitment, and indeed their performance may not necessarily require that the dancers visit sites away from the nest. All of the relocation dancers in colony D were observed in the morning hours during periods

of cool, rainy weather that prohibited flight from the hive. These dancers were either communicating sites they had visited on previous days or were performing their dances independently of any resource in the external environment. Furthermore, no dance followers left the hive during the observation periods. Third, although relocation dances were occasionally observed on three of our four swarm clusters, the majority of the dances were restricted to the swarm-preparation periods inside the natal nests. Taken together, these observations suggest that relocation dances did not trigger immediate recruitment to specific locations. Rather, they may have operated to gradually prepare colonies for mass movement by conveying the message "prepare to relocate" or "prepare to abandon the nest". Relocation dances may therefore be a component of the suite of signals and cues that mediate swarm departure from the natal nest (Pierce et al., 2007; Visscher, 2007).

Alternatively, relocation dances during reproductive swarming may be a non-functional, behavioral remnant associated with the evolution of European honey bee races. *A. mellifera* may have originated in the Middle East and Africa and then spread throughout Europe, where it gave rise to numerous subspecies adapted to temperate climates (Whitfield et al., 2006; Oldroyd and Wongsiri, 2006). Seasonal absconding, which allows colonies to following shifting resource patterns in tropical environments, is non-adaptive in temperate climates where winter survival requires remaining in a nest and amassing large food reserves (Seeley, 1985; McNally and Schneider, 1992). European races may therefore have by-and-large lost the migration dance, although a similar behavior might still occur at low (perhaps non-functional) levels during colony movements associated with swarming. At present, too little is known about the relocation dance to form conclusions about its origin or function during reproductive swarming. Nevertheless, the behavior may provide an avenue for investigating the evolution of dance communication within the genus *Apis*, as well as a means for exploring how colonies form the collective decisions that regulate mass movement.

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Les "danses de migration" dans les colonies essaimantes d'*Apis mellifera.*

***Apis mellifera* / danse frétillante / essaimage / désertion / migration saisonnière**

Zusammenfassung – Umzugstänze in schwärmenden Honigbienenvölkern, *Apis mellifera*. Der Wandertanz ist ein Tanzverhalten, das im Zusammenhang mit saisonalen Wanderschwärmen bei tropischen Bienenrassen auftritt. Wandertänze unterscheiden sich von Schwänzeltänzen durch das Fehlen des Achterlaufes und durch das Anzeigen extremer und variabler Entfernungen, hierdurch zeigen sie keine spezifischen Orte an. Eher könnten sie helfen die generelle Richtung festzulegen, in die die Kolonie letztendlich abfliegt. Bisher war angenommen worden, dass Wandertänze auf tropische Bienenrassen beschränkt sind die saisonale Wanderungen durchführen. Hier beschreiben wir dem Wandertanz ähnliche Tänze bei europäischen Honigbienen während der Vorbereitung auf das reproduktive Schwärmen.

Wir überwachten vier Beobachtungsvölker mit europäischen Bienen während der 4–7 dem natürlichen Schwärmen vorhergehenden Wochen. In jedem dieser Völker beobachteten wir 4 bis 8 Wandertänze (Tab. I). Alle Tänze traten ausschließlich innerhalb der 2 Wochen unmittelbar vor dem Schwärmen und gelegentlich auf der Oberfläche der Schwarmtrauben auf. Die Wandertänzerinnen unterschieden sich im Alter nicht von den im gleichen Zeitraum beobachteten Schwänzeltänzerinnen (P = 0,565; Tab. I). Wandertänze traten über den ganzen Tag hinweg auf und wurden von den gleichen Bienen über einen Zeitraum von 30 Minuten und mehr durchgeführt.

Die mittlere Dauer der Schwänzelläufe war bei den Wandertänzen mit 10,42 ± 1,13 s annähernd vier mal so lang wie bei den zur gleichen Zeit beobachteten Schwänzeltänzen (2,88 ± 0,32 s; P < 0,0001; Tab. I). Die Schwänzellaufdauer korrespondierte mit Entfernungen von 13197 ± 867 m beziehungsweise 3083 ± 430 m (Tab. I). Der mittlere Varianzkoeffizient der Wandertänze (31.9 ± 4.38) war fünffach größer als der der Schwänzeltänze (5,74 ± 0,59; P < 0,0001; Abb. 1). Dies deutet darauf hin, dass die Entfernungsanzeige der Schwänzelläufe in aufeinander folgenden Wandertänzen viel variabler

und ungenauer war als bei den Schwänzeltänzen. Es ist daher unwahrscheinlich, dass die Umzugstänze bestimmte Orte anzeigen.

Die Wandertänze stimmten nicht in der Anzeige einer bestimmten Richtung überein, und die von den Wandertänzerinnen angezeigten Richtungen unterschieden sich nicht von denen der Schwänzeltänzerinnen, die unterschiedliche Futterstellen besucht hatten (Abb. 2). Daher scheinen Wandertänze bei schwärmenden Völkern nicht dabei mitzuwirken, eine bestimmte Reiserichtung für das Volk festzulegen, wie es für die mit saisonalen Wanderungsbewegungen verbundenen Wandertänze von tropischen Honigbienen angenommen wird.

Unsere Untersuchung ist die erste, in der über dem Umzugtanz ähnliche Tänze bei europäischen Honigbienen oder bei irgendeiner anderen Honigbienenrasse im Zusammenhang mit reproduktiven Schwärmen berichtet wird. Da dies Tanzverhalten in der Vorbereitungsphase sowohl des reproduktiven Schwärmens als auch der saisonalen Wanderschwärme auftritt, schlagen wir vor, diese als „Umzugstänze“ neu zu charakterisieren. Obwohl die Funktion dieser Umzugstänze beim reproduktiven Schwärmen unklar ist, ist es unwahrscheinlich, dass sie bei der Wahl einer spezifischen Örtlichkeit beteiligt sind. Eher nehmen wir an, dass sie dabei beteiligt sind, das Volk auf das Verlassen des heimischen Nestes vorzubereiten.

Wandertänze / Schwänzeltanz / Schwärmen / Nestauszug / saisonale Wanderungen

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