Apidologie (1995) 26, 395-406

Original article

Swarm movement patterns inferred from waggle dance activity of the neotropical African honey bee in Costa Rica

SS Schneider

Department of Biology, University of North Carolina, Charlotte, NC 28223, USA

(Received 18 July 1994; accepted 7 July 1995)

Summary — The movement patterns of neotropical African honey bee colonies were investigated by monitoring the waggle dance activity associated with nest site selection by 10 artificially created swarm clusters. Eight of the swarms carried African mitochondrial DNA (mtDNA) and 2 had European mtDNA. The latter were classified as Africanized hybrids, *ie* European matrilines mated to African drones. Scout bees performed recruitment dances for a mean ± SD of 12.2 ± 6.6 different potential nest sites located 3 429 ± 894 m from the swarm clusters. The mean distance communicated for the nest site ultimately selected was 4 693 ± 1 728 m. Neotropical African and hybrid swarms did not differ in the number of nest sites investigated or the mean distances communicated. Swarming behavior may account for 6–18% of the total distance traveled by neotropical African bees each year.

***Apis mellifera scutellata* / Africanized honey bee / neotropical African honey bee / swarm / waggle dance / mitochondrial DNA**

INTRODUCTION

In 1956–1957 the African honey bee race, *Apis mellifera scutellata,* was introduced into Brazil (Michener, 1975; Fletcher, 1978). In the intervening 4 decades this tropically adapted bee has spread throughout South and Central America, and has recently arrived in the US (Hunter *et al,* 1993; Rinderer *et al,* 1993). *A m scutellata* will hybridize with European races, and hybrid colonies may occur at low frequencies in several neotropical regions, especially transitional zones where African swarms have invaded areas containing large, pre-existing populations of European colonies (Lobo *et al,* 1989; Del Lama *et al,* 1990; Rinderer *et al,* 1991; Sheppard *et al,* 1991a,b). However, recent DNA analyses have suggested that the neotropical honey bee remains predominantly African in genetic composition throughout most of its range in the new world (Hall and Muralidharan, 1989; Smith *et al,* 1989; Hall, 1990, 1992; Hall and Smith, 1991). Likewise, behavioral comparisons reveal few substantive differences between *A m scutellata* in Africa and the introduced African bee of Central and South America

(McNally and Schneider, 1992; McNally and Schneider, submitted for publication; Winston, 1992; Schneider and McNally, 1992a, 1994a). The ability of the neotropical African bee to rapidly colonize much of the western hemisphere while maintaining its African genetic and behavioral characteristics is one of the greatest biological success stories known. Yet, the factors contributing to this rapid spread are poorly understood.

The expansion of the neotropical Africa honey bee potentially involves 3 different types of colony movement: reproductive swarming, disturbance-induced absconding, and seasonal absconding (migration). In reproductive swarming virgin queens are produced, and the laying queen and about half the workers leave the old nest and establish in a new nest cavity (Winston, 1987). Disturbance-induced absconding occurs in response to a sudden deterioration in nest site quality due to predators, hive pests, or overheating. It does not involve the rearing of queens, and consists of an entire colony abandoning an area and moving to a new nest site (Winston *et al*, 1979; Schneider, 1990). Migration occurs during distinct times of the year, perhaps in response to deteriorating foraging conditions (McNally and Schneider, 1992; Schneider and McNally, 1992b; Winston, 1992). It also does not involve the rearing of new queens, and consists of an entire colony traveling for long distances (100 km or more), presumably to better foraging areas. Migration is preceded by several weeks of preparation in which brood rearing and foraging cease and remaining food stores are consumed (Winston *et al*, 1979; Schneider and McNally, 1992b).

All 3 types of colony movement involve the formation of swarm clusters outside the nest cavity and the use of waggle dances to determine travel patterns. In both reproductive swarming and disturbance-induced absconding, waggle dances are used to communicate the distance and direction to a variety of potential nest cavities. Eventually, all waggle dance activity becomes focused on one site, which represents the new cavity to which the colony will move (Lindauer, 1955; Seeley, 1985). During the preparation period associated with seasonal absconding, workers perform 'migration dances', which communicate extreme, but highly variable distances, and are not associated with food sources (Schneider and McNally, 1994b). Migration dances do not become focused upon one particular location, yet upon departure colonies travel in the direction in which the majority of their dances were concentrated (Schneider and McNally, 1994b). Waggle dance activity therefore provides a valuable tool for examining the movement patterns of neotropical honey bee swarms.

It is unknown how far reproductive, absconding and migrating swarms travel in the neotropics. Likewise, it is unclear to what extent the different types of movement have contributed to the rapid spread of the neotropical African bee. Indeed, unless swarms issue from colonies of known developmental histories, it is difficult to distinguish among reproductive, absconding and migrating swarms in the field and thus to determine the type of movement that is being observed. In the present study, we artificially created swarms and monitored their waggle dances associated with selecting a new nest cavity. Such manipulations stimulate the nest site selection process associated with reproductive swarming and disturbance-induced absconding (Lindauer, 1955; Robinson and Dyer, 1993).

MATERIALS AND METHODS

Study site

The study was conducted from June to July 1993 near Bagaces in Guanacaste, Costa Rica (10°

31.6'N; 85° 19.3'W). The study period coincided with the migration season and the onset of the reproductive swarming season. Thus, colonies were examined during natural periods of movement in Costa Rica.

Establishing swarms and determining colony type

Swarm clusters were created following the methods of Robinson and Dyer (1993). The queen of a colony was caged and suspended on a 2 m pole. The workers were then shaken onto the ground and quickly clustered about the queen. Waggle dances for potential new nest sites typically began to occur within several hours of swarm formation. A total of 10 colonies were utilized, collected within a 60 km radius of the study site. The collection location and original condition of each colony (swarm; naturally occurring nest; managed hive) are presented in table I. None of the colonies originally occurring within a nest cavity exhibited indications of reproductive swarming, absconding or migration at the time of collection, and thus were not already preparing for movement prior to swarm establishment (see McNally and Schneider, 1992; Schneider and McNally, 1992b for methods of determining colony movement preparations). Colonies 3 and 4 were collected as swarms (table I) and thus their histories were unknown. All swarms were estimated by visual inspection to contain 4 000–7 000 bees.

Neotropical African honey bees have been in Costa Rica for approximately a decade, and naturally occurring colonies exhibit behaviors and growth patterns typical of *A m scutellata* in Africa (Spivak, 1991). However, hybrid colonies (crosses between neotropical African and European honey bees) are maintained in apiaries and may become feral. Morphometric and mitochondrial DNA (mtDNA) analyses were therefore used to determine the nature of the swarms used in this study. Once each swarm cluster was established, 20–25 individual workers were collected at random and preserved in 90% ethyl alcohol. Morphometric analyses were conducted at the Honey Bee Breeding, Genetics and Physiology Laboratory, Baton Rouge, LA. Ten workers from each swarm were measured for 20 different characters, and the resulting data were analyzed with the discriminate analysis program, USDA-ID (Stelzer, personal communication). This program generates posterior probabilities that samples belong to the Africanized group *(pA)*, which are interpreted as follows: $0.990 \leq pA \leq 1.000$ Africanized (possessing predominantly African-like traits); $0.900 \leq$

Table I. The collection location, initial condition, morphometric classification, and mtDNA classification for each of the swarms examined.

Swarm	*Collection location*	*Original condition*	*Morphometric classification*	*mtDNA classification*
1	Bagaces	Natural nest	A	African
2	Bagaces	Natural nest	A	African
3	Juntas	Swarm	A	African
4	Santa Ana	Swarm	A	African
5	Bagaces	Hive	A	African
6	Santa Ana	Hive	A	African
7	Santa Ana	Hive	A	African
8	Bagaces	Natural nest	A	African
9	Bagaces	Hive	AE	European
10	Bagaces	Hive	A	European

Collection location represents the town nearest to (within 1–6 km) the collection site; natural nest refers to unmanaged colonies occupying natural or man-made cavities; hive refers to managed colonies maintained in man-made hive boxes. A = Africanized; AE = Africanized with evidence of the introgression of European genes.

$pA \leq 0.990$ Africanized with evidence of introgression of European genes; $0.500 \leq pA \leq 0.900$ European with evidence of introgression of Africanized genes; $0.000 \leq pA \leq 0.500$ European.

The mtDNA identifications were done by HG Hall using a method based on the polymerase chain reaction (Hall and Smith, 1991). Mitochondrial DNA is maternally inherited and non-recombining (Moritz *et al*, 1987; Hall, 1991). Therefore, workers with African mtDNA will have been produced by an African queen. Conversely, workers from an Africanized colony that possess European mtDNA are hybrids resulting from a cross between a European queen and African drones. In this study colonies containing workers with African mtDNA were classified as neotropical African; those with European mtDNA were classified as hybrids. Nuclear DNA analysis was not conducted, and thus some workers classified as neotropical African may have been hybrids of an African queen and European drones. Also, the number of generations that the colonies with European mtDNA may have backcrossed with African drones was not known. However, this study examined colony movements, and several authors have suggested that mtDNA may influence colony dispersal ability (Hall, 1990; Harrison and Hall, 1993). Thus, classifications in the present study were based on mtDNA.

All morphometric and mtDNA analyses were conducted after the study ended, and thus the nature of each colony was not known during data collection. However, colonies 3, 4, 5, 9 and 10 were originally suspected of being hybrids, because they came from or near apiaries that were occasionally stocked with hybrid queens.

To ensure that suitable nest cavities were available within the study area, ten 13.5 L cardboard swarm traps equipped with vials of pheromone were established at 150–200 m increments within a 1 km radius of the swarms. Pheromone-baited traps are regularly used to attract swarms in Central and South America, and are readily accepted as nest cavities by honey bees (Schmidt *et al*, 1989; Schmidt and Thoenes, 1990). All swarm traps were located within riparian woodland, which is the preferred nesting habitat of *A m scutellata* in Costa Rica (Schmidt, personal communication). The traps were checked for occupancy 1–2 times each week and any invading ant or wasp colonies were removed. The traps were also examined for occupancy within 12–24 h after each swarm departed from the experimental set-up.

Monitoring waggle dance activity and determining the route of colony travel

Waggle dance activity was monitored on the swarm clusters for 30 min each hour from 0800 to 1700 h each day until the swarm departed. During each 30 min observation period, waggle dancers were selected at random, and I determined for each: (1) the distance and direction communicated; and (2) whether the dances indicated a food site, a non-food (nest) site, or were migration dances. As far as was possible, each observed bee was marked on the thorax or abdomen with a dot of non-toxic paint to determine the total number of different dancers for each indicated site.

In the waggle dance the straight run portion (the waggle-run) communicates the distance and direction to resources (von Frisch, 1967; Michelsen *et al*, 1992). 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; Michelsen *et al*, 1992). The direction indicated by each observed dancer on the swarm clusters was determined 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.

The distance indicated by each dancer was determined by timing a mean ± SD of 8.1 ± 10.6 consecutive waggle-runs using a digital stopwatch, and then calculating a mean waggle-run duration. For marked bees that danced for the same site during more than one 30 min observation period, a mean was calculated over all observed waggle-runs. Mean waggle-run durations were then converted into distance estimates in meters, using 'standard curves' established by (1) training marked workers from swarms 2, 5 and 9 to feeding stations at known distances up to 1 200 m from the swarms; and then (2) timing their waggle-runs once they returned to the swarm clusters (see Schneider, 1990; Schneider and McNally, 1992b, 1994b for further descriptions of measuring and translating waggle-run durations). The translation of dance times greater than those covered by the standard curves was accomplished by extrapolation, following the methods of Dyer and Seeley (1991).

A dancer was considered to indicate a food site if it carried pollen loads or offered samples of nectar to followers during dance performance. Dancers not carrying pollen loads or offering nectar samples were considered to be associated with potential nest sites. A migration dancer was defined as a bee whose mean waggle-run duration communicated a distance ≥ 8 km, but whose consecutive waggle-runs were highly variable and indicated distances that differed by 1 km or more (Schneider and McNally, 1994b). Non-food site dancers that indicated distances ≥ 8 km, but whose consecutive waggle-runs were of consistent duration, were considered to be associated with potential nest sites.

For each swarm a recruitment map was constructed by plotting the location communicated by each observed waggle dancer (see Schneider, 1989, 1990, for examples of recruitment maps generated from waggle dance activity). The maps were used to determine: (1) the total number of different nest sites visited; (2) the number of dancers recruiting for each nest site; and (3) the mean ± SD distance (m) communicated over all visited nest sites. Additionally, the maps were used to determine (4) the distance and direction of the 'final destination' for each swarm, defined as the one specific site on which all waggle dance activity became focused prior to departure. Dances for food sites and migration dances were excluded from the analyses of nest site locations. The different parameters measured from the recruitment maps were compared within and between the neotropical African and hybrid swarms groups using Student's *t*-tests and nested analysis of variance.

Once all dancers on a swarm were indicating the same site, the queen was released from the cage. The direction in which each swarm flew upon departure was recorded using a magnetic compass.

Unless stated otherwise all mean values are reported as ± 1 SD. Distance estimates were log-transformed prior to analysis to ensure homogeneity of variances.

RESULTS

The morphometric analysis suggested that swarms 1–8 and 10 were Africanized (pA for each > 0.998), while swarm 9 was Africanized with evidence of the introgression of European genes ($pA < 0.927$; table I). The mtDNA analysis revealed that swarms 1–8 possessed African mtDNA, while swarms 9 and 10 possessed European mtDNA (table I). Swarm 10 was the only colony that was classified differently by the 2 analyses. However, based on mtDNA this colony was classified as an African–European hybrid in all of the data analyses.

The standard curves constructed for the relationship between waggle-run duration and distance of swarms 2, 5 and 9 are given in figure 1. The curves for swarms 2 and 5 were combined and used to estimate the distances communicated in the neotropical African swarms. The curve for swarm 9 was used for the 2 hybrid colonies.

A total of 306 different dancers were observed over all 10 swarms, 284 (93%) of which were classified as associated with potential nest sites. Of the remaining 22 dancers, 9 indicated food sites and 13 were migration dancers. Each swarm focused recruitment entirely on one specific nest site within 1–3 d of establishment. The observed waggle dance activity was therefore similar to that associated with reproductive swarming and disturbance-induced absconding. There was no evidence that the experimental manipulations stimulated migration behavior.

A examination of the recruitment maps revealed that the swarms investigated multiple potential nest cavities over a large area of the environment, and traveled relatively great distances fo their final destinations. No differences were observed between the neotropical African and hybrid colonies for any of the dance parameters examined (nested ANOVA used for all comparisons; $F < 0.25$; $P > 0.60$). Thus, the data were combined over all 10 swarms, although the nature of each swarm is indicated in the tables and figures.

The colonies recruited for a mean of 12.2 ± 6.6 different nest sites (table II). The

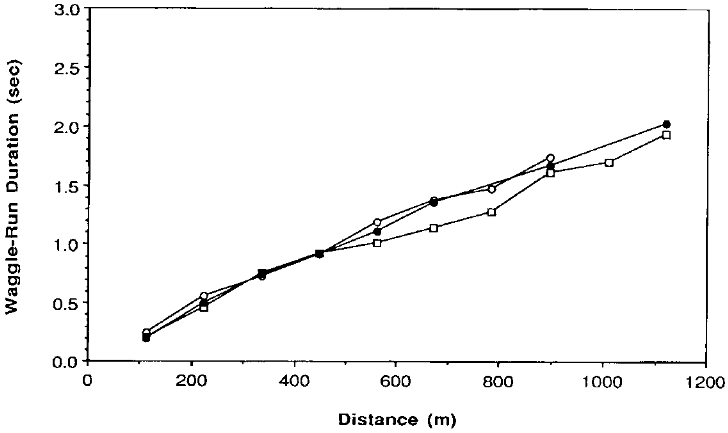

Fig 1. The relationship between distance and waggle-run duration for 3 of the swarms examined. Colony 2 (O), colony 5 (●), colony 9 (□).

mean distance communicated to potential nest sites was 3 429 ± 894 m. Of the 122 total nest sites indicated, 47 (38.5%) occurred more than 4 km from the swarm clusters; only 11 (9%) occurred within 1 km.

A nested ANOVA revealed a highly significant difference in the mean distance communicated within (but not between) the neotropical African and hybrid groups ($F = 6.98$; $P < 0.001$; table II).

Table II. The total number of observed waggle dancers for nest sites, number of different nest sites recruited for, and the mean ± SD distance communicated over all dancers for the neotropical African and hybrid swarms.

	Total dancers	*Sites*	*Distance communicated (m)*
Neotropical African colonies			
1	32	12	3 575 ± 1 402
2	18	7	3 621 ± 746
3	13	3	2 726 ± 2 536
4	15	6	1 803 ± 749
5	48	23	4 590 ± 2 833
6	17	10	4 775 ± 1 459
7	22	10	3 933 ± 1 675
8	30	12	3 135 ± 933
Hybrid colonies			
1	44	17	2 730 ± 1 185
2	45	22	3 400 ± 1 553

The mean distance communicated for the final destinations was 4 693 ± 1 728 m. Seven of the swarms selected nest sites more than 4 km away; 3 chose sites more than 6 km from the swarm locations (fig 2). A nested ANOVA revealed a highly significant difference in the mean distances communicated by colonies within (but not between) the 2 groups ($F = 56.7$; $P < 0.001$; fig 2).

Upon departure each swarm flew in the direction indicated by the waggle dances for the final destination. None of the swarm set up within 1 km of the study site was occupied by the experimental colonies, which would have been identifiable by the marked waggle dancers.

DISCUSSION

Neotropical African and hybrid swarms in northwestern Costa Rica searched for new nest cavities over relatively large areas of the environment, and communicated (and by inference traveled) a mean distance of 4.7 km to the sites ultimately selected. Reproductive swarms of *A m scutellata* in Botswana, Africa may also dance for nest site 3 or more kilometers away (Schneider and McNally, 1993). Thus, the distances communicated in the present study may be typical of *A m scutellata* and its new world descendants when selecting nesting sites under the environmental conditions examined.

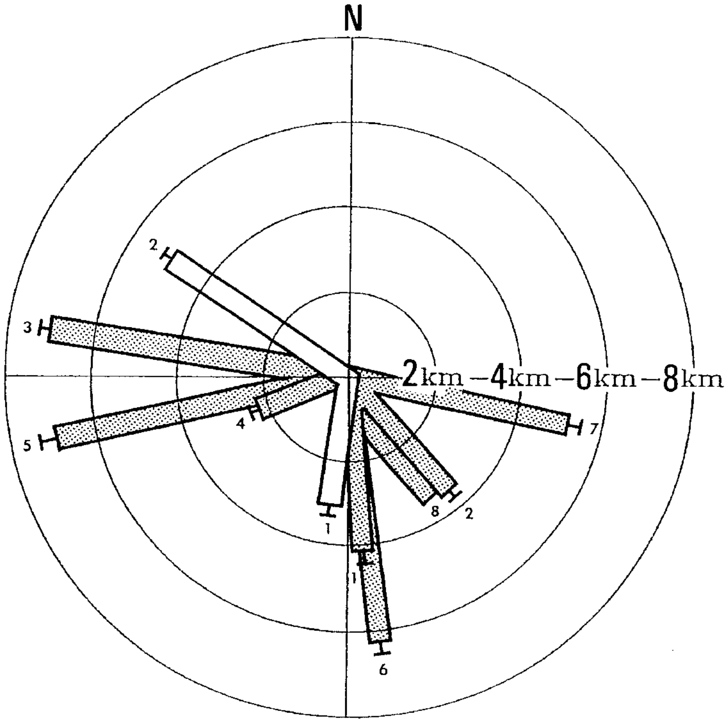

Fig 2. The distance and direction communicated for the final destinations of the neotropical African swarms (shaded bars) and hybrid swarms (open bars). The number at the top of each bar is the swarm identification number.

The distance that honey bee swarms travel to nest sites may be influenced by a variety of factors, including the availability of nest cavities and the distribution of forage (Winston, 1987). It is unlikely that the 4.7 km communicated by dancers in the present study resulted from a shortage of nest cavities within the immediate study area. Suitable nest boxes were supplied within a 1 km radius of the swarms, yet none of these was selected as a final destination. It is also unlikely that the colonies traveled long distances in response to a local shortage of floral resources. A major source of nectar for honey bees in Costa Rica, *Baltimora ricta,* was in bloom throughout much of the study period, and several large fields of this species occurred within 1–2 km of the study site. Indeed, 2 locations within 2 km of the study area had previously been used for managed hives, which thrived and produced large honey stores (Stewart, personal communication). Other factors which were not examined in the present study may have influenced nest site selection. Nevertheless, the available data suggest that the distances communicated by the Costa Rican swarms may not have occurred solely in response to local resource or nesting conditions, and thus may have reflected to some extent a movement preference. Swarm movement preferences have also been suggested for several European honey bee races (Jaycox and Parise, 1980, 1981; Gould, 1982). However, the distances traveled to new nest sites by African colonies will need to be examined in other neotropical and African areas before definite conclusions can be drawn.

In contrast to the Costa Rican swarms, swarms of European honey been races in temperate regions usually travel distances of only 0.2–0.6 km, and rarely 1–2 km (Seeley and Morse, 1977; Jaycox and Parise, 1980, 1981; Gould, 1982; Schmidt and Thoenes, 1990). However, these studies have been conducted in radically different habitats, and thus it is unknown to what extent the travel distances result from differing environmental conditions or racially mediated factors. Comparisons need to be made within the same habitat to determine if there are any inherent differences in the movement patterns of African and European colonies.

Despite the relatively large distances traveled by swarms in Costa Rica, it is unlikely that nest site selection has played the major role in the rapid spread of the neotropical African bee. The average rate of range expansion throughout South and Central America has been 160–500 km per year (Otis, 1991). If one assumes 6 reproductive swarm movements per year (Taylor, 1977; Otis, 1982, 1991) and a mean travel distance of 4.7 km per movement, then nest site selection associated with reproductive swarming can account for 6–18% of the total distance traveled each year. However, this represents only a rough estimate, because swarms might travel greater distances in areas of poorer forage. Furthermore, at present the annual rate of disturbance-induced absconding for neotropical African colonies is unknown. Nevertheless, the available data suggest that the major factor contributing to the spread of the neotropical African bee may be seasonal migratory movements.

European matrilines that have become Africanized are typically rare in the advancing front of neotropical African bees (Hall and Muralidharan, 1989; Smith *et al,* 1989; but see Rinderer *et al,* 1991). In the present study too few Africanized hybrid colonies were examined to allow for definitive comparisons of the movement patterns of neotropical African and hybrid swarms. However, waggle dance activity provides a powerful tool for making such comparisons, and for determining if the paucity of swarms with European mtDNA in the advancing front is influenced by different movement patterns between the 2 colony types.

ACKNOWLEDGMENTS

I thank J Harrison, HG Hall and 3 anonymous reviewers for comments on the manuscript, JA Stelzer (United States Department of Agriculture, Honey Bee Breeding, Genetics and Physiology Research, Baton Rouge, LA) for conducting the morphometric analyses, HG Hall for the mtDNA determinations, and L Leamy for statistical advice. The Stewart Ranch in Guanacaste kindly allowed the study to be conducted on their property. G Frankie arranged for lodging and a vehicle, and provided valuable technical support. I give special thanks to my assistant, N Campos. The study was funded by a Seed Grant from the United States Department of Agriculture (Grant No 92-37106-7990).

Résumé — Étude des mouvements d'essaims déduits de l'activité de danse frétillante chez l'abeille africaine néotropicale au Costa Rica. Les déplacements d'essaims des colonies d'abeilles africaines néotropicales ont été analysés à Guanacaste au Costa Rica par enregistrements des danses frétillantes associées à la sélection des nouveaux nids. Dix essaims ont été créés artificiellement selon la méthode de Robinson et Dyer (1993). L'analyse morphométrique a montré que 9 de ces essaims étaient africanisés tandis qu'un seul (essaim n°9) était africanisé avec introgression de gènes d'abeilles de races européennes (tableau I). L'analyse de l'ADN mitochondrial (ADNmt) a révélé que 8 de ces essaims possédaient de l'ADNmt africain alors que 2 (n° 9 et 10) possédaient de l'ADNmt européen (tableau I). En se basant sur l'ADNmt, les essaims 1 à 8 ont été classés comme étant des abeilles néotropicales et les essaims 9 et 10 comme étant des hybrides d'abeilles africaines et européennes. Dix boîtes de nidification de 13,5 l contenant de la phéromone de piégeage ont été disposées dans un rayon de 1 km autour des essaims afin de s'assurer que des cavités de nidification étaient disponibles dans la région proche. Les activités de danse frétillante ont été enregistrées par périodes de 30 min chaque jour jusqu'à ce que les essaims partent, ce qui a permis de calculer la distance et la direction communiquées par chaque danseuse. Les distances ont été estimées en utilisant les «courbes standard» qui avaient été établies au cours d'expériences préalables menées avec les essaims 2, 5 et 9 (fig 1). Les courbes des essaims 2 et 5 ont été associées et utilisées pour estimer les distances communiquées par les essaims africains néotropicaux; la courbe de l'essaim 9 a été utilisée pour les 2 colonies hybrides. Les essaims ont exploré de nombreuses cavités situées dans de vastes régions et ont voyagé sur des distances relativement grandes jusqu'à leurs destinations finales. En moyenne, pour les 10 essaims, les éclaireuses des colonies recrutent pour 12,2 ± 6,6 sites de nidification représentant une distance moyenne de 3 429 ± 894 m. Pour le nid finalement choisi, la distance moyenne est de 4 693 ± 1 728 m (tableau II, fig 1). Aucun des essaims n'a choisi les nids artificiels placés dans un rayon de 1 km. Aucune différence significative n'a été observée entre les abeilles africaines et les hybrides pour aucun des paramètres examinés ($p > 0,05$ pour toutes les comparaisons). Il est invraisemblable que les grandes distances parcourues par ces essaims résultent d'une pénurie de sites de nidification ou de ressources florales dans la région étudiée. De plus, de grandes surfaces de *Baltimora ricta* (une importante source de nectar pour les abeilles au Costa Rica) étaient en fleurs dans un rayon de 1 à 2 km. Sauf si d'autres facteurs non pris en compte dans cette étude ont influencé les déplacements des essaims, nos résultats suggèrent que les distances relativement grandes communiquées par les essaims costaricains reflètent davantage un choix pour ces distances qu'une réponse aux conditions locales. En dépit de ces grandes distances, la sélection du site de nidification ne compte vraisemblablement que pour 6–18% de la distance totale réalisée chaque année par les abeilles africaines néotropicales (d'après un calcul basé sur une expansion moyenne de 160–500 km par an, 6 essaimages par an, et une distance moyenne parcourue de 4,7 km par déplacement). Cela suggère que le facteur principal qui contribue à l'expansion rapide de ces abeilles est l'existence de mouvements migratoires saisonniers.

***Apis mellifera scutellata* / abeille africanisée / abeille africaine néotropicale / essaim / danse frétillante / ADN mitochondrial**

Zusammenfassung — Ermittlung der Schwarmbewegungen aus den Schwänzeltänzen bei neotropischen afrikanischen Honigbienen auf Costa Rica. Die Bewegung von Schwärmen neotropischer afrikanischer Bienen wurde durch Beobachtung der Schwänzeltanzaktivität und die Untersuchung der Auswahl von Nistplätzen in Guanacaste, Costa Rica ermittelt. Insgesamt wurden 10 Kunstschwärme nach der Methode von Robinson und Dyer (1993) hergestellt. Nach dem Ergebnis einer morphometrischen Analyse waren 9 der Schwärme afrikanisiert, während einer (Schwarm 9) einen deutlichen Einfluss europäischer Gene zeigte (Tabelle I). Eine Analyse mitochondrialer DNS (mtDNA) wies für 8 der Schwärme afrikanische, für die anderen 2 europäische mtDNA nach (Schwarm 9 und 10). Auf Grundlage der mtDNA wurden Schwarm 1–8 als neotropische afrikanische, Schwarm 9 und 10 als afrikanisch-europäische Hybriden klassifiziert. Um sicherzustellen, daß in dem Untersuchungsbereich passende Nistplätze vorhanden waren, wurden innerhalb eines Umkreises von 1 km 10 mit Pheromonködern versehene Schwarmfangkästen aufgestellt.

Die Schwänzeltänze wurden bis zum Abflug der Schwärme täglich 30 min lang erfasst. Die von jeder beobachteten Tanzbiene angezeigte Richtung und Entfernung wurde ermittelt. Die Entfernungen wurden anhand von zuvor in Trainingsexperimenten für Schwarm 2, 5, und 9 (Abb 1) erstellten Standardkurven des Zusammenhangs zwischen Schwänzeltanzdauer und Entfernung abgeschätzt. Die zusammengefassten Kurven von Schwarm 2 und 5 wurden für die neotropischen afrikanischen Bienen, die Kurve von Schwarm 9 für die beiden Hybridkolonien verwendet.

Die Tanzbienen zeigten eine Vielzahl möglicher Nesthöhlen (12,2 ± 6,6, Mittelwert und Standardabweichung für alle 10 Schwärme) in einem weiten Bereich der Umgebung an (alle angezeigten Nisthöhlen: 3429 ± 894 m) und legten relativ weite Strecken bis zu ihrem endgültigen Bestimmungsort zurück (4693 ± 1728 m für die am Ende ausgewählte neue Nisthöhle). Keiner der Schwärme bezog eine der im Umkreis von 1 km aufgestellten Schwarmfangkästen. Die neotropischen afrikanischen und die Hybridkolonien unterschieden sich in keinem der gemessenen Parameter (getestete ANOVA; $P > 0.05$ für alle Vergleiche).

Es ist unwahrscheinlich, daß die von den experimentellen Schwärmen zurückgelegten Entfernungen durch einen Mangel an Nisthöhlen oder des Blütenangebotes hervorgerufen wurden, da die im Umkreis von 1 km aufgestellten geeigneten Schwarmfangkästen unbesiedelt geblieben waren. Während eines Großteils der Untersuchungszeit blühten in einem Umkreis von 1–2 km um den Bereich der Studie umfangreiche Felder mit *Baltimora ricta,* eine Hauptnektarquelle der Honigbienen auf Costa Rica. Obwohl andere nichtuntersuchte Faktoren die Schwarmbewegungen beeinflußt haben könnten, legt das Ergebnis dieser Studie nahe, daß die relativ großen angezeigten Entfernungen eher auf die bevorzugte Schwarmbewegung der Bienen auf Costa Rica zurückzuführen sind als auf eine Reaktion auf die örtlichen Gegebenheiten.

Trotz der in dieser Studie relativ großen von den Schwärmen angezeigten Entfernungen ist die Wahl eines Nistplatzes wahrscheinlich nur für 6–18% der von neotropi-

schen afrikanischen Bienen zurückgelegten Gesamtentfernung verantwortlich, wie sie sich aus einer mittleren Ausbreitungsgeschwindigkeit von 160–500 km pro Jahr, sechs Schwarmbewegungen und einer mittleren zurückgelegten Entfernung von 4,7 km errechnet. Hierdurch wird nahegelegt, daß saisonale Wanderungen den Hauptfaktor für die schnelle Ausbreitung neotropischer afrikanischer Bienen darstellen.

***Apis mellifera scutellata* / afrikanisierte Honigbiene / Schwarm / Schwänzeltanz**

REFERENCES

Del Lama MA, Lobo JA, Soares AEE, Del Lama SN (1990) Genetic differentiation estimated by isozymic analysis of Africanized honeybee populations from Brazil and from Central America. *Apidologie* 21, 271-280

Dyer FC, Seeley TD (1991) Dance dialects and foraging range in three Asian honey bee species. *Behav Ecol Sociobiol* 28, 227-233

Fletcher DJC (1978) The African honey bee, *Apis mellifera adansonii*, in Africa. *Ann Rev Entomol* 23, 151-171

Frisch K von (1967) *The Dance Language and Orientation of Bees.* Harvard University Press, Cambridge, MA, USA

Gould JL (1982) Why do honey bees have dialects? *Behav Ecol Sociobiol* 10, 53-56

Hall HG (1990) Parental analysis of introgressive hybridization between African and European honeybees using nuclear DNA RFLPs. *Genetics* 125, 611-621

Hall HG (1991) Genetic characterization of honey bees through DNA analysis. *In: The "African" Honey Bee* (M Spivak, DJC Fletcher, MD Breed, eds), Westview Press, San Francisco, CA, 45-73

Hall HG (1992) DNA studies reveal processes involved in the spread of new world African honeybees. *Florida Entomol* 75, 51-59

Hall HG, Muralidharan K (1989) Evidence from mitochondrial DNA that African honey bees spread as continuous maternal lineages. *Nature (Lond)* 339, 211-213

Hall HG, Smith DR (1991) Distinguishing African and European honeybee matrilines using amplified mitochondrial DNA. *Proc Natl Acad Sci USA* 88, 4548-4552

Harrison JF, Hall HG (1993) African-European honeybee hybrids have low nonintermediate metabolic capacities. *Nature (Lond)* 363, 258-260

Hunter LA, Jackman JA, Sugden EA (1993) Detection records of Africanized honey bees in Texas during 1990, 1991 and 1992. *Southwest Entomol* 18, 79-89

Jaycox ER, Parise SG (1980) Homesite selection by Italian honey bee swarms, *Apis mellifera ligustica* (Hymenoptera: Apidae). *J Kans Entomol Soc* 53, 171-178

Jaycox ER, Parise SG (1981) Homesite selection by swarms of black-bodied honeybees, *Apis mellifera caucasica* and *A m carnica* (Hymenoptera: Apidae). *J Kans Entomol Soc* 54, 697-703

Koeniger N, Koeniger G (1980) Observations and experiments on migration and dance communication of *Apis dorsata* in Sri Lanka. *J Apic Res* 19, 21-34

Lindauer M (1955) Schwarmbienen auf Wohnungssuche. *A Vergleich Physiol* 37, 263-324

Lobo JA, Del Lama MA, Mestriner MA (1989) Population differentiation and racial admixture in the Africanized honeybee (*Apis mellifera* L). *Evolution* 43, 794-802

McNally LC, Schneider SS (1992) Seasonal cycles of growth, development and movement of the African honey bee, *Apis mellifera scutellata,* in Africa. *Insectes Soc* 39, 167-179

Michelsen A, Andersen BB, Strom J, Kirchner WH, Lindauer M (1992) How honeybees perceive communication dances, studied by means of a mechanical model. *Behav Ecol Sociobiol* 30, 143-150

Michener CD (1975) The Brazilian bee problem. *Ann Rev Entomol* 20, 339-416

Moritz C, Dowling TE, Brown WM (1987) Evolution of animal mitochondrial DNA: relevance for population biology and systematics. *Ann Rev Ecol Syst* 18, 269-292

Otis GW (1982) Population biology of the Africanized honey bee. *In: Social Insects of the Tropics, Vol 1* (P Jaisson, ed), université Paris-Nord, Paris, 209-219

Otis GW (1991) Population biology of the Africanized honey bee. *In: The "African" Honey Bee* (M Spivak, DJC Fletcher, MD Breed, eds), Westview Press, San Francisco, CA, 213-234

Rinderer TE, Stelzer JA, Oldroyd BP, Buco SM, Rubnik WL (1991) Hybridization between European and Africanized honey bees in the neotropical Yucatan peninsula. *Science* 253, 309-311

Rinderer TE, Oldroyd BP, Sheppard WS (1993) Africanized bees in the US. *Sci Am* 269, 84-90

Robinson GE, Dyer FC (1993) Plasticity of spatial memory in honey bees: reorientation following colony fission. *Anim Behav* 46, 311-320

Schmidt JO, Thoenes SC (1990) The efficiency of swarm traps: what percent of swarms are captured and at what distance from the hive. *Am Bee J* 130, 811-812

Schmidt JO, Thoenes SC, Hurley R (1989) Swarm traps. *Am Bee J* 129, 468-471

Schneider SS (1989) Spatial foraging patterns of the African honey bee, *Apis mellifera scutellata. J Insect Behav* 2, 505-521

Schneider SS (1990) Nest characteristics and recruitment behavior of absconding colonies of the African honey bee, *Apis mellifera scutellata*, in Africa. *J Insect Behav* 3, 225-240

Schneider S, Blyther R (1988) The habitat and nesting biology of the African honey bee, *Apis mellifera scutellata,* in the Okavango River Delta, Botswana, Africa. *Insectes Soc* 35, 167-181

Schneider SS, McNally LC (1992a) Seasonal patterns of foraging activity in colonies of the African honey bee, *Apis mellifera scutellata*, in Africa. *Insectes Soc* 39, 181-193

Schneider SS, McNally LC (1992b) Factors influencing seasonal absconding in colonies of the African honey bee, *Apis mellifera scutellata. Insectes Soc* 39, 403-423

Schneider SS, McNally LC (1993) Spatial foraging patterns and colony energy status in the African honey bee, *Apis mellifera scutellata. J Insect Behav* 6, 195-210

Schneider SS, McNally LC (1994a) Developmental patterns associated with founding and swarming in colonies of the African honey bee race, *Apis mellifera scutellata* Lepeletier. *Apidologie* 25, 530-539

Schneider SS, McNally LC (1994b) Waggle dance behavior associated with seasonal absconding in colonies of the African honey bee, *Apis mellifera scutellata. Insectes Soc* 41, 115-127

Seeley TD (1985) *Honeybee Ecology.* Princeton University Press, Princeton, NJ, USA

Seeley TD, Morse RA (1977) Dispersal behavior of honey bee swarms. *Psyche* 83, 199-209

Sheppard WS, Rinderer TE, Mazzoli JA, Stelzer JA, Shimanuki H (1991a) Gene flow between African- and European-derived honey bee populations in Argentina. *Nature (Lond)* 349, 782-784

Sheppard WS, Soares AEE, DeJong D, Shimanuki H (1991b) Hybrid status of honey bee populations near the historic origin of Africanization in Brazil. *Apidologie* 22, 643-652

Smith DR, Taylor OR, Brown WM (1989) Neotropical Africanized honey bees have African mitochondrial DNA. *Nature (Lond)* 339, 213-215

Spivak M (1991) The Africanization process in Costa Rica. *In: The "African" Honey Bee* (M Spivak, DJC Fletcher, MD Breed, eds), Westview Press, San Francisco, CA, 137-155

Taylor OR (1977) Past and possible future spread of Africanized honey bees in the Americas. *Bee World* 58, 19-30

Winston ML (1987) *The Biology of the Honey Bee.* Harvard University Press, Cambridge, MA, USA

Winston ML (1992) The biology and management of Africanized honey bees. *Ann Rev Entomol* 37, 173-193

Winston ML, Otis GW, Taylor OR (1979) Absconding behaviour of the Africanized honeybee in South America. *J Apic Res* 18, 85-94