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Research article

Seasonal nest usurpation of European colonies by African swarms in Arizona, USA

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Summary. Nest usurpation is a form of reproductive parasitism that may contribute to the ability of African bees to displace European honey bees in the Americas. We examined nest usurpation by African swarms over a two-year period in a southern-Arizona apiary that contained 76 five-frame European colonies. We observed a mean annual usurpation rate of 21%, with strong seasonal trends in usurpation activity. Most usurpations occurred from October–December, with a minor peak of usurpation activity in the spring-summer months. The seasonal patterns of usurpation corresponded with the reproductive swarming season in spring and summer and the absconding season in the fall-winter months. Queenless colonies, colonies that contained a queen confined in a cage, and those that had been recently requeened were 2–8 times more likely to be invaded than were colonies that contained an actively laying queen, suggesting that queen condition may have a major influence on host-colony susceptibility to usurpation. This trend was particularly pronounced in October–December, during which months the usurpation rates experienced by caged-queen and queenless colonies approached 20–50%. Our results show that nest usurpation is seasonally frequent among honey bees in the southwestern U.S., which suggests that reproductive parasitism contributes to the invasion success of African honey bees and possibly other introduced social insect species.

Key words: Usurpation, colony takeover, reproductive parasitism, African honey bee, *Apis mellifera scutellata.*

Introduction

Reproductive parasitism is wide spread in the highly social insects and may have influenced the evolution of colony defense mechanisms, nest-mate and kin-recognition abilities and pheromonal communication systems (Hölldobler and Wilson, 1990; Turillazzi et al., 2000; Lenoir et al., 2001; Sledge et al., 2001; D'Ettorre et al., 2002). An extreme example of reproductive parasitism is found in the African race of honey bees, *Apis mellifera scutellata* Lepeletier, which can exhibit 'nest usurpation' (also known as colony takeover). During usurpation, a small African swarm invades a colony and replaces the resident queen (Danka and Rinderer, 1988; Dietz et al., 1989). Usurpation is unique to African bees; European honey bee swarms do not invade other colonies. Nest usurpation may contribute to the ability of African bees to displace European bees in the New World, and has repeatedly been proposed as a mechanism to account for the loss of European characteristics in invaded areas of the neotropics and the southwestern U.S. (Hall, 1999; Clarke et al., 2001, 2002). Nest usurpation therefore provides a valuable system for examining reproductive parasitism in social bees, as well as the role that this phenomenon may play in biological invasions by introduced insect species. However, usurpation remains one of the least understood aspects of African honey bee biology (Schneider et al., 2004). In particular, nest usurpation has never been examined in the U.S., despite the fact that African bees now exist as large, expanding populations throughout the southwestern states and parts of California (Visscher et al., 1997; Hall, 1999; Loper et al., 1999; Loper, 2002).

There has been considerable debate over the importance of nest usurpation in the spread of African bees in different regions of the neotropics (Gonçalves et al., 1974; Taylor, 1985; Camazine, 1986; Danka and Rinderer, 1988; Hall and Muralidharan, 1989; Vergara et al., 1993). Annual usurpation rates reported for managed European colonies in Latin America vary from 0%–40% and often show pronounced year-to-year fluctuations (Danka et al., 1992; Vergara et al., 1993). Nest usurpation can also exhibit considerable seasonal variation (Vergara et al., 1993), which may provide a starting point for understanding the role that reproductive parasitism plays in the annual colony cycle of African bees in the Americas. However, the factors that contribute to regional and seasonal patterns of nest usurpation have received little attention.

We also have a limited understanding of how usurpation swarms locate and gain entry into susceptible host colonies. European colonies that are small, stressed, queenless or contain a failing queen may have an increased risk of usurpation (Danka and Rinderer, 1988; Otis, 1991; Hellmich and Rinderer, 1991; Rinderer and Hellmich, 1991; Vergara et al., 1993). Colonies with a queen confined in an 'excluder cage' (a common management practice for introducing new queens) may also have a greater susceptibility to takeover (Danka and Rinderer, 1988; Hellmich and Rinderer, 1991; Rinderer and Hellmich, 1991). Thus, cues associated with compromised colony condition or queen performance may be used by usurpation swarms to locate susceptible hosts. However, strong queenright European colonies (those with a laying queen) can also be usurped (Danka et al., 1992; Vergara et al., 1993), which suggests that additional factors may also influence the likelihood of takeover. Usurpation swarms often cluster below the colony entrance and then enter the nest several h or days later (Rinderer and Hellmich, 1991; Vergara et al., 1993), which may provide a period in which colony susceptibility is assessed. Entry into the colony can involve fighting between usurping bees and host workers (authors' personal observations), although the role of aggression during colony takeover is not well understood.

We had the opportunity to examine nest usurpation in an apiary of European colonies maintained over a two-year period, as part of a long-term study of African bees in Tucson, AZ. The African bee arrived in Arizona in 1993 and has subsequently established large populations that contain few or no European matrilines (Loper et al., 1999; Fewell and Bertram, 2002). The study apiary therefore provided an opportunity to examine the impact of nest usurpation on managed European colonies that are increasingly challenged by a growing feral African population. Our study had two main objectives. First, we determined the incidence and seasonal patterns of usurpation in the managed apiary. Second, we examined the influence of colony strength and queen condition on host colony susceptibility to usurpation.

Materials and methods

The study was conducted from May 2001 through April 2003 at the Carl Hayden Bee Research Center in Tucson, AZ. Nest usurpation was monitored in an apiary that contained 76 five-frame European 'nucleus' colonies. Each colony was headed by a European queen that had been commercially reared and mated in 'African-bee free' areas of the U.S.

The European queens used in our study colonies were open-mated 'Golden Italian' queens that expressed the cordovan (*cd*) cuticular coloration. The workers exhibited the 'light blond' coloration and indistinct abdominal banding patterns characteristic of the Golden Italian line. These light coloration patterns contrast sharply with those of feral African colonies in the study area, which typically exhibit either solid black coloration or a dark cuticular color with a distinct dark band on each abdominal segment. The African identity of feral colonies showing the dark coloration patterns have been repeatedly confirmed by morphometric and mtDNA analyses (DeGrandi-Hoffman et al., 1998a, b; 2003; Schneider and DeGrandi-Hoffman, 2002; 2003). The color differences between *cd* and African bees therefore allow for the reliable discrimination of bee types and have been used to examine the influence of African and European characteristics on worker defensive behavior (DeGrandi-Hoffman et al., 1998a), queen development time (DeGrandi-Hoffman et al., 1998b), queen fighting ability (Schneider and DeGrandi-Hoffman, 2003) and worker-queen interactions (Schneider and DeGrandi-Hoffman, 2002; 2003). Furthermore, we mitotyped four small swarms showing the dark coloration patterns that were collected from our study area (see Nielson et al., 1999; 2000 for methodology). All were identified as African. Thus, our use of the cordovan marker, in combination with the fact that only African swarms invade other colonies, allowed us to reliably distinguish between European hosts and usurping African bees.

Each queen was paint marked on the thorax when introduced into a nucleus hive. All colonies were treated for the parasitic mite, *Varroa destructor*, and other diseases following standard protocols and subjected to standard management practices, as described below.

We monitored colony strength and queen condition throughout the study period by conducting weekly or bi-weekly inspections. During each inspection, we determined for each colony if the original paint-marked queen was present. We also assigned a rating to each colony for the amount of brood comb present and worker population size, as follows: A: three or more frames of comb filled with brood of all stages and four or more frames covered by workers; B: 2.5–3 frames of brood and 3–4 frames covered by workers; C: 1.5–2 frames with a well-defined brood pattern and 2–3 frames covered by workers; D: one or fewer frames of brood and 1–2 frames of workers; F: little or no brood with an erratic brood pattern and less than one frame of workers.

During the inspections, colonies were classified as thriving, weak, queenless or invaded. A colony was identified as thriving if it contained the original paint-marked Golden Italian queen and received a rating of C or better for both brood comb area and worker population size. Thriving colonies that were preparing for swarming were divided. The original paint-marked queen and half the workers were retained in the study apiary and the remainder of the colony was moved to a different bee yard. All queen cells in the retained colonies were destroyed and inspections were conducted repeatedly throughout the following two weeks to remove overlooked queen cells and all newly emerged virgin queens.

A colony was considered to be weak if it contained a paint-marked Golden Italian queen, but received a rating below C for brood comb area and worker population size. For weak colonies, the queen was removed and a new, mated Golden Italian queen was introduced under a wire-mesh push-in cage. Newly introduced queens were confined under the push-in cages for 4–6 days and then released. This re-queening procedure is typically used to maintain colony vigor in managed apiaries and has been suggested to contribute to the usurpation of European colonies (Hellmich and Rinderer, 1991; Rinderer and Hellmich, 1991).

Colonies that became queenless during the study were allowed to raise replacement queens, to determine if queenlessness and queen rearing influenced the likelihood of takeover. However, virgin queens were not allowed to become the new laying queens of their colonies because they would have mated with at least some African drones and caused the colonies to become Africanized. Each queenless colony was checked repeatedly and all emerged virgin queens were destroyed and replaced with paint-marked, mated Golden Italian queens to ensure that each colony remained European throughout the study period.

A colony was considered to have been invaded if we found a dark-colored African queen and at least 30–50 dark workers inside the nest. The invading bees were clearly distinguishable from the light-yellow host workers and the yellow, paint-marked host queens. After the usurpation event had been recorded, we removed the invading African queen and, if the host queen had been eliminated, the colony was re-queened with a paint marked European queen. In this manner we maintained a constant number of European nucleus colonies throughout the study period.

To determine annual rates and seasonal patterns of usurpation, we first examined each year of the study separately. We next examined the combined data for the entire 24-month study period and calculated a mean annual usurpation rate and mean monthly rates. This approach allowed us to examine year-to-year variation in usurpation activity, as well as assess general seasonal trends.

We examined the effects of colony strength and queen condition on host susceptibility as follows. For each month of the study, we determined the number of usurped and non-usurped colonies in four categories: colonies that were thriving, weak, queenless, and that contained a caged queen or had been re-queened within the preceding two week period. We then compared the monthly proportions of colonies that experienced usurpation events using 4 × 2 × 2 contingency tables [4 colony categories × 2 categories of usurpation (usurped and non-usurped) X 2 years] analyzed by log-linear models (Sokal and Rohlf, 1995). All means are reported as ± one SE.

Results

Rates and seasonal patterns of usurpation

We observed a total of 32 colony takeovers during the study period. The annual usurpation rates for years 1 and 2 were 30.3% and 11.8%, respectively (mean usurpation rate: 21.1 ± 9.3%). The mean monthly usurpation rate over both years was 1.7 ± 0.5%.

There was marked variation in the temporal patterns of usurpation activity observed for the two years of the study (Fig. 1). However, when viewed over the entire 24-month period several seasonal trends were suggested for colony takeovers (Fig. 2). First, usurpations occurred in all months of the year except for January and February. Second, the greatest usurpation activity occurred from October through December. This period accounted for 56% of the total usurpation events observed and had mean monthly usurpation rates of approximately 3%–5% (Fig. 2). The fall-winter peak was especially pronounced in year 1 and occurred to a lesser extent in year 2 of the study (Fig. 1). Third, there was a secondary peak of usurpation activity from April through August, which accounted for 37.5% of colony takeovers and had mean monthly usurpation rates of approximately 1%–2% (Fig. 2). However, there was considerable variability between the two years in the spring-summer months in which usurpations were observed.

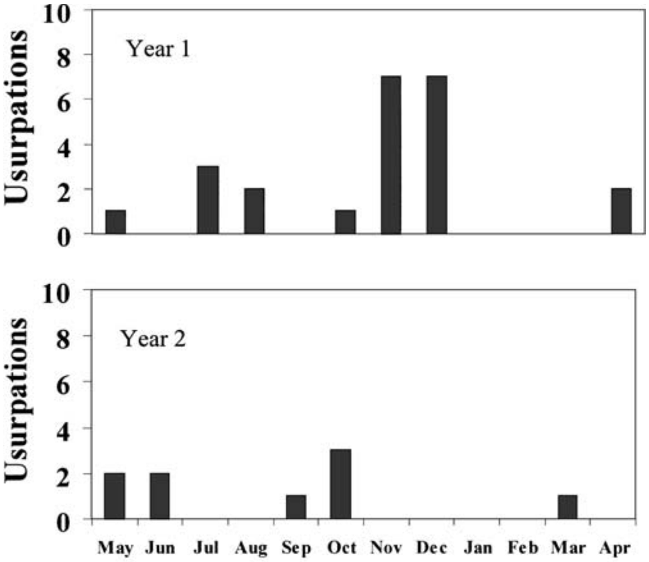

Figure 1. Number of usurpations observed during each month of the two years of the study. Year 1 consisted of the period from May 2001 through April 2002; Year 2 consisted of the period from May 2002 through April 2003

Host colony strength, queen condition and susceptibility to usurpation

Colonies in all categories of strength and queen condition experienced usurpation events (Table 1). However, there was a significant difference among colony categories (Chi-square = 8.91; df = 3; P = 0.0306) that was associated primarily with queen condition. When viewed over the entire study period, the monthly usurpation rates for queenless colonies were 6–8 times greater than those for thriving and weak colonies (Table 1). Usurpation rates for colonies that contained a caged-queen and had been recently re-queened were 2–3 times greater that those for thriving and weak colonies. In general, queenless colonies accounted for 6% of the total colonies examined each month, but experienced

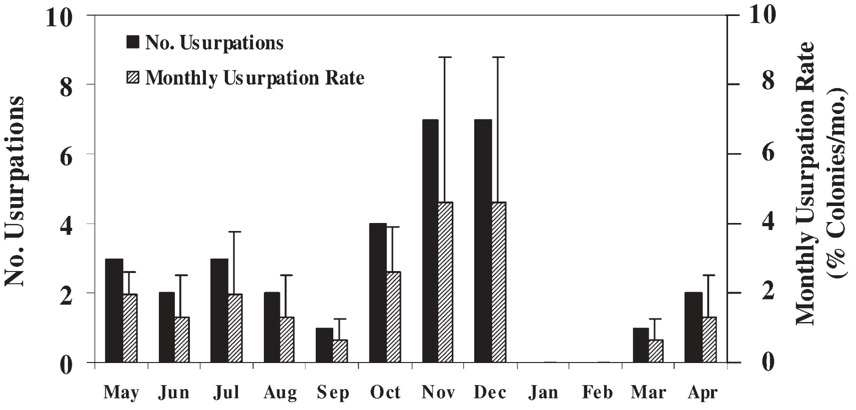

Figure 2. The monthly totals for usurpation events (solid bars) and the mean ± SE monthly usurpation rates (% colonies/month; shaded bars) for both years of the study combined

Table 1. The mean ± SE number of colonies each month exhibiting the different categories of strength and queen condition, the total usurpation events occurring within each category, and the monthly usurpation rates experienced by each category for the entire 24-month study period, the fall-winter months (October–December), and the spring-summer months (April–August). Colonies were categorized as caged queen/re-queened if they were usurped while containing a caged queen or within two weeks following the release of a caged queen. The proportions of usurped colonies in each category during the different periods were compared using log-linear models. The months of January and February were excluded from the analyses because no usurpations occurred during these months in either year of the study

Colony Condition	Colonies/mo.	Total Usurpation Events	Usurpation Rates (% colonies/mo)		
			Overall	Fall-Winter	Spring-Summer
Thriving	45.6 ± 3.15	8	1.61 ± 1.15	4.95 ± 4.48	1.00 ± 0.71
Weak	12.1 ± 2.85	6	2.23 ± 1.43	2.47 ± 2.04	4.17 ± 4.20
Queenless	4.4 ± 0.91	8	12.78 ± 6.25	50.0 ± 28.9	11.43 ± 5.95
Caged queen/ re-queened	13.9 ± 2.70	10	5.50 ± 2.70	16.7 ± 9.65	2.12 ± 1.68

25% of the total usurpations observed; caged-queen and re-queened colonies comprised 18% of the total colonies, but accounted for 31% of usurpation events (Table 1). These trends were similar during both years of the study (Chi-square = 0.55; df = 3; P = 0.908).

The association between queen condition and host susceptibility varied seasonally. During October–December, the mean usurpation rate for queenless colonies (50%) was 10–20 times greater than that for thriving and weak colonies, and the rates for caged-queen and re-queened colonies were 6–7 times greater (Chi-square = 12.91; df = 3; P = 0.0048; Table 1). In contrast, usurpation rates during the spring and summer months did not differ among the colony groups (Chi-square = 6.04; df = 3; P = 0.110), although queenless colonies still experienced a rate that was 3–10 times higher than that of the other categories (Table 1). Thus, the effect of queen condition on host susceptibility was most pronounced during the fall and winter months and occurred to a lesser extent during the remainder of the year. Thriving and weak colonies could be usurped throughout the year at similar, low monthly rates of 1–5% (Table 1).

Discussion

We observed annual usurpation rates ranging from 12%–30% in the Tucson region. It could be argued that our rates were inflated because we used small colonies of cordovan bees, which may have had an increased susceptibility to takeover. The cordovan trait has been associated with reduced viability in drones (Tucker, 1986; Berg et al., 1997) and could potentially weaken a colony and lower its resistance to usurpation. However, there is no known association between the *cd* trait and any aspect of worker or queen viability (Taber and Wendell, 1958; Tucker, 1986; Schneider and DeGrandi-Hoffman, 2002, 2003), and *cd* queens are regularly produced for commercial sale (Koehnen, 1999; Glenn and Glenn, 2001). Furthermore, we found no difference in the rates at which strong and weak colonies were usurped. Similarly, Vegara et al. (1993) studied large European colonies and found that weak colonies were not at greater risk of takeover. Danka et al. (1992) and Vergara et al. (1993) examined colony takeovers in Venezuela and Mexico using large European colonies that did not express the cordovan characteristic, and reported annual usurpation rates of 5% and 0–40%, respectively. Thus, the usurpation rates we observed for our small cordovan colonies fell within the range reported previously for larger, non-cordovan colonies in Latin America. Our results are therefore likely to reflect the nest usurpation rates of full-sized European colonies in southern Arizona.

We observed strong seasonal patterns of usurpation activity that may have been related to the annual colony cycle of African bees in southern Arizona. The minor peak of usurpation activity observed in the spring and summer months coincided with the primary swarming season for honey bees in the Tucson area (Schmidt, 1995). In contrast, the major peak of usurpation activity in October–December may have coincided with seasonal absconding by African colonies. Seasonal absconding is a non-reproductive process that consists of an entire colony abandoning a nest in response to deteriorating foraging conditions and traveling for up to 100 km, presumably to relocate to an area with greater floral resources (Winston et al., 1979; Schneider and McNally, 1992; 1994; Winston, 1992). The mountains surrounding the Tucson basin harbor a large population of feral African colonies (Loper et al., 1999) and forage availability at these higher elevations declines during the fall and winter months. This may result in large-scale absconding into the Tucson basin, where agricultural and horticultural activities result in increased floral abundance during this period (Wardell, pers. comm.). Many usurpation swarms may therefore be small reproductive or absconding African swarms that would have a low probability of surviving if they attempted to establish their own nest, especially during fall and winter. Rather, these swarms may adopt a strategy of invasion and reproductive parasitism, and this tendency may be particularly pronounced during seasonal absconding. Thus, nest usurpation may be an important component of the annual colony cycle that contributes to the spread of African bees in the Tucson region. Usurpation swarms in Latin America have also been suggested to be small reproductive swarms and absconding swarms (Danka and Rinderer, 1988; Rinderer and Hellmich, 1991), although their association with the annual colony cycle of African bees has never been examined in the neotropics.

Host colony susceptibility to usurpation was strongly influenced by queen condition. Our queenless colonies experienced usurpation rates that were many times greater than those of colonies with laying queens, especially during October–December. Higher usurpation rates associated with queenlessness have also been reported for European colonies in Latin America (Danka and Rinderer, 1988; Hellmich and Rinderer, 1991; Rinderer and Hellmich, 1991; Vergara et al., 1993). We also found elevated rates of usurpation for caged-queen and recently re-queened colonies. Although several authors have suggested such an association (Danka and Rinderer, 1988; Hellmich and Rinderer, 1991; Rinderer and Hellmich, 1991), our study is the first to demonstrate that queen replacement involving the caging of queens increases host susceptibility to takeover.

The greater susceptibility of queenless and caged-queen colonies suggests that cues associated with queen reproductive performance and brood rearing could be used by usurpation swarms to locate susceptible hosts. Perhaps usurpation swarms respond to reduced levels of brood pheromone. This could help to explain the increased usurpation rates for queenless and caged-queen colonies in which brood rearing is interrupted, as well as the greater usurpation rates observed during the fall and winter when brood production is reduced. Furthermore, Hooper et al. (submitted) found that queens produce volatile compounds that vary with egg laying activity. Thus, it is possible that volatile compounds reflect queen reproductive performance and could be used by usurpation swarms to locate susceptible hosts. However, the fact that some strong colonies with large amounts of brood can also be invaded suggests that no single factor determines host susceptibility to usurpation.

Taken in concert, the associations between queen condition, season, and usurpation activity may have implications for the methods used to maintain strong European colonies in invaded regions. The most commonly utilized practice for maintaining European colonies is re-queening annually with mated European queens. The first step in re-queening a colony is to remove the laying queen and wait several days before introducing the new queen. The introduced queen is typically caged in the colony for several days and then released. Our study indicates that re-queening colonies during certain times of the year could, instead of reducing the chance of 'Africanization,' actually increase vulnerability to becoming African due to usurpation. While the times when usurpation events were most frequent in our study may not be representative of all areas where African bees might establish, identifying when swarming and absconding by feral African colonies occurs in a given region and avoiding re-queening at those times could be critical to maintaining colonies with European matrilines.

Our study suggests that nest usurpation plays an important, but annually variable role in the loss of European characteristics in the southwestern U.S. Because of migratory beekeeping and commercial queen-rearing practices, nest usurpation in the southwestern states could potentially result in the transportation of African matrilines to other regions of the country (Schneider et al., 2004). However, our understanding of nest usurpation is too rudimentary to draw firm conclusions about its role in the spread of African honey bees in the U.S. Usurpation rates should be examined for managed colonies in different habitats in the southwestern states, to assess more fully the regional variation in colony takeovers and the possible contribution of human activity to the process. To fully evaluate the role of usurpation in the invasion process, usurpration rates should be compared in regions that are newly colonized by the advancing 'front' of African swarms to those that harbor established African populations. Additionally, future research should focus on the role of chemical signals in usurpation and the ability of invading swarms to displace resident queens. Such work should help us to understand, not only the mechanisms that mediate reproductive parasitism, but also the contribution of social parasitism in the establishment and spread of introduced social insect species.

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References

Berg, S., N. Koeniger and S. Fuchs, 1997. Body size and reproductive success of drones (*Apis mellifera* L.). *Apidologie 28*: 449–460.

Camazine, S., 1986. Queen rearing in São Paulo State, Brazil: a beekeeping experience of over 20 years. *Am. Bee J. 126*: 414–416.

Clarke, K.E., B.P Oldroyd, G. Qeuzada-Euán and T.E. Rinderer, 2001. Origin of honey bees (*Apis mellifera* L.) from the Yucatan peninsula inferred from mitochondrial DNA analysis. *Molec. Ecol. 10*: 1347–1355.

Clarke, K.E., T.E. Rinderer, P. Franck, J.G. Quezada-Euán and B.P. Oldroyd, 2002. The Africanization of honey bees (*Apis mellifera* L.) of the Yucutan: A study of a massive hybridization event across time. *Evolution 56*: 1462–1474.

Danka, R.G. and T.E. Rinderer, 1988. Social reproductive parasitism by Africanized honey bees. In: *Africanized Honey Bees and Bee Mites* (G.R. Needham, R.E. Page, Jr., M. Delfinado-Baker and C.E. Bowman, Eds), John Wiley and Sons, New York, pp. 214–222.

Danka, R.G., R.L. Hellmich R.L. and T.E. Rinderer, 1992. Nest usurpation, supersedure and colony failure contribute to Africanization of commercially managed European honey bees in Venezuela. *J. Apic. Res. 31*: 119–123.

D'Ettorre, P.D., N. Mondy, A. Lenoir and C. Errard, 2002. Blending in with the crowd: social parasites integrate into their host colonies using a flexible chemical signature. *Proc. R. Soc. Lond. B 269*: 1911–1918.

DeGrandi-Hoffman, G., D.R. Tarpy and S.S. Schneider, 2003. Patriline composition of worker populations in honeybee (*Apis mellifera*) colonies headed by queens inseminated with semen from African and European drones. *Apidologie 34*: 111–120.

DeGrandi-Hoffman, G., A.M. Collins, J.H. Martin, J.O. Schmidt and H.G. Spangler, 1998a. Nest defense behavior in colonies from crosses between Africanized and European honey bees. *J. Insect Behav. 11*: 37–45.

DeGrandi-Hoffman, G., J.C. Watkins, A.M. Collins, G.M. Loper, J.H. Martin, M.C. Arias and W.S. Sheppard, 1998b. Queen developmental time as a factor in the Africanization of European honey bee

(Hymenoptera: Apidae) populations. *Ann. Entomol. Soc. Am. 91*: 52–58.

Dietz, A., C. Vergara, M. Mejia and R. Krell, 1989. Forced queen usurpation in colonies of Africanized and European honey bees in Argentina. Proc. 32nd Apimondia Int. Congr., Rio de Janeiro, Brazil, Apimondia Publishing House, Bucharest, Romania, pp. 88–92.

Fewell, J.H. and S.M. Bertram, 2002. Evidence for genetic variation in worker task performance by African and European honey bees. *Behav. Ecol. Sociobiol*. *52*: 318–325.

Glenn, T. and S. Glenn, 2001. Cordovan: Bees of a different color. http://members.aol.com/queenb95/cordovan.html.

Gonçalves, L.S., W.E. Kerr, J. Chaud Netto and A.C. Stort, 1974. Some comments on the 'Final report of the committee on the African honey bee – National Research Council – N.A.S. 1972'. Department of Entomology, Cornell Univ., Ithaca, NY.

Hall, H.G., 1999. Genetic and physiological studies of African and European honey bee hybridizations: past, present and into the 21st century. In: *Apiculture for the 21st Century* (R. Hoopingarner and L. Connor, Eds), Wicwas Press, Cheshire, CT, pp. 52–59.

Hall, H.G. and K. Muralidharan, 1989. Evidence from mitochondrial DNA that African honey bees spread as continuous maternal lineages. *Nature 339*: 211–213.

Hellmich, R.L. and T.E. Rinderer, 1991. Beekeeping in Venezuela. In: *The "African" Honey Bee* (M. Spivak, D.J.C. Fletcher and M.D. Breed, Eds), Westview Press, San Francisco, pp. 399–411.

Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Harvard Univ. Press, Cambridge, MA. 732 pp.

Koehnen, C.F. and Sons, Inc., 1999. *Our Bee Process*. http://www.koehnen.com/process.htm.

Lenoir, A., P. D'Ettorre, C. Errard and A. Hefetz, 2001. Chemical ecology and social parasitism in ants. *Ann. Rev. Entomol*. *46*: 573–599.

Loper, G.M., 2002. Nesting sites, characterization and longevity of feral honey bee colonies in the Sonoran Desert of Arizona: 1991–2000. In: *Proc. 2nd Int. Conf. Africanized Honey Bees and Bee Mites* (E.H. Erickson, Jr, R.E. Page, Jr and A.A. Hanna, Eds), A.I. Root, Medina, OH, pp. 86–96.

Loper, G.M., J. Fewell, D.R. Smith, W.S. Sheppard and N. Schiff, 1999. Changes in the genetics of a population of feral honey bees (*Apis mellifera* L.) in S. Arizona after the impact of tracheal mites (*Acarapis woodi*), Varroa mites (*Varroa jacobsoni*) and Africanization. In: *Apiculture for the 21st Century* (R. Hoopingarner and L. Connor, Eds), Wicwas Press, Cheshire, CT, pp. 47–51.

Nielsen, D.I., P.R. Ebert, G.J. Hunt, E. Guzmán-Novoa, S.A. Kinnee and R.E. Page Jr, 1999. Identification of Africanized honey bees (Hymenoptera: Apidae) incorporating morphometrics and an improved polymerase chain reaction mitotyping procedure. *Ann. Entomol. Soc. Am. 92*: 167–174.

Nielsen, D.I., P.R. Ebert, R.E. Page Jr, G.J. Hunt and E. Guzmán-Novoa, 2000. Improved polymerase chain reaction-based mitochondrial genotype assay for identification of the Africanized honey bee (Hymenoptera: Apidae). *Ann. Entomol. Soc. Am*. *93*: 1–6.

Otis, G., 1991. Population biology of the Africanized honey bee. In: *The 'African' Honey Bee* (M. Spivak, D.J.C. Fletcher and M.D. Breed, Eds), Westview Press, San Francisco, pp. 213–234.

Rinderer, T.E. and R.L. Hellmich II, 1991. The process of Africanization. In: *The 'African' Honey Bee* (M. Spivak, D.J.C. Fletcher and M.D. Breed, Eds), Westview Press, San Francisco, pp. 95– 117.

Schmidt, J.O., 1995. Dispersal distance and direction of reproductive European honey bee swarms (Hymenoptera: Apidae). *J. Kansas Entomol. Soc*. *68*: 320–325.

Schneider, S.S. and L.C. McNally, 1992. Factors influencing seasonal absconding in colonies of the African honey bee, *Apis mellifera scutellata*. *Insect. Soc. 39*: 403–423.

Schneider, S.S. and L.C. McNally, 1994. Waggle dance behavior associated with seasonal absconding in colonies of the African honey bee, *Apis mellifera scutellata. Insect. Soc. 41*: 115–127.

Schneider, S.S. and G. DeGrandi-Hoffman, 2002. The influence of worker behavior and paternity on the development and emergence of honey bee queens. *Insect. Soc*. *49*: 306–314.

Schneider, S.S. and G. DeGrandi-Hoffman, 2003. The influence of paternity on virgin queen success in hybrid colonies of European and African honey bees. *Anim. Behav. 65*: 883–892.

Schneider, S.S., G. DeGrandi-Hoffman and D.R. Smith, 2004. The African honey bee: Factors contributing to a successful biological invasion. *Ann. Rev. Entomol*. *49*: 351–376.

Sledge, M.F., F.R. Dani, R. Cervo, L. Dapporto and S. Turillazzi, 2001. Recognition of social parasites as nest-mates: adoption of colony-specific host cuticular odours by the paper wasp parasite *Polistes sulcifer*. *Proc. R. Soc. Lond. B 268*: 2253–2260.

Taber, S.III and J. Wendel, 1958. Concerning the number of times queen bees mate. *J. Econ. Entomol. 51*: 786–789.

Taylor, O.R., 1985. African bees: potential impact in the United States. *Bull. Entomol. Soc. Am. 31*: 15–24.

Tucker, K.W., 1986. Visible mutants. In: *Bee Genetics and Breeding* (T.E. Rinderer, Ed), Academic Press, Orlando, FL, USA. pp. 57–90.

Turillazzi, S., M.F. Sledge, F.R. Dani, R. Cervo, A. Massolo and L. Fondelli, 2000. Social hackers: Integration in the host chemical recognition system by a paper wasp social parasite. *Naturwissenschaften 87*: 172–176.

Vergara, C., A. Dietz and A. Perez de Leon, 1993. Female parasitism of European honey bees by Africanized honey bee swarms in Mexico. *J. Apic. Res*. *32*: 34–40.

Visscher, P.K., R.S. Vetter and F.C. Baptista, 1997. Africanized bees, 1990–1995: Initial rapid expansion has slowed in the U.S. *Calif. Agric*. *51*: 22–25.

Winston, M.L., 1992. *Killer Bees: The Africanized Honey Bee in the Americas*. Harvard Univ. Press, Cambridge, MA. 162 pp.

Winston, M.L., G.W. Otis and O.R. Taylor, 1979. Absconding behaviour of the Africanized honey bee in South America. *J. Apic. Res*. *18*: 85–94.