

Research article

Queen replacement in African and European honey bee colonies with and without afterswarms

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Abstract. We examined the dynamics of the queen replacement process in African and European colonies that did and did not produce afterswarms. In colonies without afterswarms, the queen replacement process was completed in 24–48 hours, the first-emerging virgin queen (VQ) typically inherited the natal nest even if multiple queens emerged, workers performed few vibration signals on emerged queens, and all signaling activity was directed toward early emerging VQs. In contrast, if colonies did produce afterswarms, the queen replacement process required 5–6 days, there was no advantage for first-emerging queens, vibration rates on emerged queens were 25 times greater, and signaling activity was directed toward all VQs. Although vibration signal activity was more pronounced in colonies with afterswarms, the signal was consistently associated with increased VQ survival under all conditions. These trends were exhibited similarly in the African and European colonies, suggesting that they have broad applicability to queen-replacement decisions over a range of environmental and racial conditions. However, the African and European colonies differed in the total number of queens involved in the elimination process and the relative importance of queen duels and pre-emergence destruction under the different reproductive strategies. Taken together, our results suggest that worker behavior is a major determinant for the outcome of queen replacement, either through reduced interactions that allow first-emerged queens to rapidly eliminate rivals, or through increased use of interactions such as the vibration signal, which may allow workers to influence the ultimate fate of each emerged VQ. We discuss the possibility that these behavior patterns may reflect the roles of cooperation and conflict in shaping honey bee reproductive decisions.

Keywords: Vibration signal, queen replacement, afterswarm, swarming, social reproduction.

Introduction

Worker-queen interactions in social insects often have a major influence on colony organization and social reproductive decisions (Tarpy and Gilley, 2004; Tarpy et al., 2004; Ratnieks et al., 2006). In the honey bee, *Apis mellifera*, worker-queen interactions can be particularly pronounced during queen replacement, which occurs under two conditions: (1) when a laying queen begins to fail or dies, and (2) during reproductive swarming, when the laying queen and about half the workers leave the natal nest in a “primary swarm” and move to a new nest cavity (Winston, 1987). Under both conditions, workers in the natal nest rear multiple virgin queens (VQs) in specially constructed queen cells. When the VQs emerge, some may leave in secondary swarms, called “afterswarms.” The remaining VQs battle among themselves until there is a sole survivor who becomes the new laying queen of the natal nest. Virgin queens eliminate one another through pre-emergence destruction, in which emerged VQs sting unemerged rivals through the walls of their queen cells, and through “duels,” in which two emerged VQs battle until one is stung to death (Gilley, 2001, 2003; Gilley and Tarpy, 2005). Honey bee workers do not kill emerged VQs themselves, but will interact with them at high rates through chasing, biting and the performance of vibration signals (Schneider et al., 2001; Gilley, 2003; Gilley and Tarpy, 2005). Many of these interactions may prevent or delay pre-emergence destruction and duels, and may have a major influence on the final outcome of the queen replacement process

(Schneider and Lewis, 2004; Tarry and Gilley, 2004; Gilley and Tarry, 2005). Queen replacement has profound effects on colony survival, genetic structure, and worker inclusive fitness, and is therefore likely to be under strong selection pressures operating at the levels of the individual queen, individual sterile worker, and the colony as a whole (Visscher, 1993; Tarry et al., 2004).

Workers and queens may follow different strategies for gaining genetic benefits during queen replacement, and the degree to which these strategies diverge or align may depend upon whether a colony produces afterswarms (Visscher, 1993). If a colony is too small to produce afterswarms, either because of a diminished worker population following the departure of the primary swarm or reduced colony growth resulting from queen failure, it may be necessary to replace the queen as quickly as possible to minimize the interruption to brood rearing. Under these conditions, only one VQ needs to emerge and survive, and the genetic interests of workers and queens may be more aligned. In colonies without afterswarms, the first VQ to emerge often quickly eliminates her rivals through pre-emergence destruction and has few interactions with workers, resulting in a brief replacement process (Gilley and Tarry, 2005). In contrast, when a colony produces afterswarms, two or more VQs must emerge and survive, one to depart with each afterswarm and one to inherit the natal nest. Under these conditions, workers and queens may be in conflict. Virgin queens will experience the greatest success by inheriting the natal nest with its vast reserves of resources, and should attempt to remain in the nest and eliminate rivals as quickly as possible (Visscher, 1993). Workers, on the other hand, should attempt to keep several VQs alive throughout the afterswarming process, and influence the timing of queen fights and which VQs depart or remain in the nest. In colonies with afterswarms, the first queen to emerge does not necessarily have a survival advantage, workers often interact with emerged VQs at high rates, and the elimination period may be more protracted (Schneider et al., 2001; Gilley and Tarry, 2005). The afterswarming process therefore provides an opportunity to explore caste interactions in colony reproductive decisions, as well as investigate the relative importance of different levels of selection in shaping honey bee reproductive decisions. However, worker-queen interactions in colonies following the different reproductive strategies have only recently received detailed investigation (Gilley and Tarry, 2005).

The purpose of our study was to examine queen replacement in colonies that did and did not produce afterswarms. We had two main goals. First, we compared the dynamics of queen replacement in colonies pursuing the two strategies by determining: (1) the total duration of the rival elimination period, (2) the number of queens produced and the relative importance of pre-emergence destruction versus duels in VQ elimination, (3) the influence of emergence order on VQ survival, and (4) the degree to which workers interacted with emerged

queens. For the fourth factor, we focused on the vibration signal, which is one of the most frequently occurring worker-queen interactions during the elimination period and may influence VQ survival by allowing workers to delay or interrupt queen fights (Schneider et al., 2001; Schneider and DeGrandi-Hoffman, 2003). Our second goal was to compare the influence of afterswarming on the dynamics of queen replacement in African and European races of honey bees. African and European honey bees are adapted to tropical and temperate-climate habitats, respectively (McNally and Schneider, 1996). African bees have higher reproductive rates and swarm more frequently than European bees, and may have different patterns of worker-queen interactions (Schneider et al., 2004; Gilley and Tarry, 2005). Comparisons between the races may therefore provide insights into the flexibility of the queen replacement process in colonies adapted to different ecological conditions and life history strategies.

Methods and materials

Study sites and colony set up: To fully assess the dynamics of the queen replacement process, it is necessary to monitor queen behavior continuously from the moment the first VQ emerges until there is a sole inheritor of the natal nest, which may require several days of round-the-clock observations. This limits the number of colonies in any one investigation, and thus it is often necessary to combine results from different studies to obtain a sufficient sample size of VQs to detect general trends in queen replacement (Schneider et al., 2001; Gilley and Tarry, 2005). Our study reports the compiled data from three separate investigations, one conducted in the Okavango River Delta, Botswana, Africa (Schneider, 1991), one on the campus of the University of North Carolina, Charlotte, NC (Painter-Kurt and Schneider, 1998), and the third at the Carl Hayden Bee Research Center, Tucson, AZ (Schneider et al., 2001; Schneider and DeGrandi-Hoffman, 2003). The three studies examined 21 different colonies maintained in observation hives (Table 1). Nine of the colonies were classified as African-matriline colonies: two were *Apis mellifera scutellata* colonies monitored in Botswana and seven were hybrid colonies headed by African queens mated to African and European drones maintained in Tucson, AZ (Table 1). African-matriline hybrid colonies are behaviorally nearly identical to "pure" *A. m. scutellata* colonies (Schneider et al., 2004), and we therefore considered them to be African. The remaining 12 colonies were classified as European-matriline colonies and consisted primarily of the European race, *A. m. ligustica*. Two of the European colonies were monitored in Charlotte, NC and 10 were monitored in Tucson, AZ. Two of the colonies swarmed naturally, while the remaining 19 produced virgin queens in response to the experimental removal of the laying queen, and afterswarms were produced under both conditions (Table 1). The 21 colonies produced a total of 194 sealed queen cells: 61 gave rise to emerged virgin queens and 133 were eliminated through pre-emergence destruction (Table 1). Thus, although the colonies in the different studies did not experience the same genetic or environmental conditions, they provided a large sample of rival queens that allowed an examination of general trends in queen replacement in colonies that followed different reproductive strategies. Worker-queen interactions in the study colonies have been reported previously (Schneider, 1991; Schneider et al., 2001; Schneider and DeGrandi-Hoffman, 2003); however, the results presented here are novel.

The methods of monitoring VQ behavior and worker-queen interactions have been previously reported (Schneider, 1991; Schneider et al., 2001) and are briefly summarized below. Emerged VQs were monitored round-the-clock (subdivided into 30 min periods) and for each we determined: (1) her emergence order (1st, 2nd, etc., to emerge in

Table 1. The number of afterswarms produced, total virgin queens (VQs) reared, number of emerged VQs, emergence order (1st, 2nd, etc.) for each surviving VQ, number of VQs killed in pre-emergence destruction, and the number of emerged VQs eliminated in duels for each of the 21 colonies examined. For Colony Designation, the first letter indicates race (A: African; E: European), the second entry location (BT: Botswana; AZ: Arizona; NC: North Carolina), and the final number indicates the individual colony.

Colony Designation	Afterswarms produced	Total VQs Reared	Emerged VQs	Emergence Order of Surviving VQs	VQs Killed Pre-emergence	VQs Killed in Duels
AFRICAN COLONIES						
A-BT-1 ^a	1	4	2	1 ^{st*} , 2 ^{nd**}	2	0
A-BT-2 ^a	1	7	5	2 ^{nd*} , 5 ^{th**}	2	3
A-AZ-3 ^b	1	7	4	3 ^{rd*} , 4 ^{th**}	3	2
A-AZ-4 ^b	0	12	1	1 ^{st**}	11	0
A-AZ-5 ^b	0	12	2	1 ^{st**}	10	1
A-AZ-6 ^b	0	9	6	2 ^{nd**}	3	5
A-AZ-7 ^b	0	14	1	1 ^{st**}	13	0
A-AZ-8 ^b	0	3	1	1 ^{st**}	2	0
A-AZ-9 ^b	0	7	1	1 ^{st**}	6	0
Total (Mean±SE/colony)						
with Afterswarms	3	18 (6.0 ± 1.0)	11 (3.7 ± 0.88)	1 1 st -emerging VQ survived	7 (2.3 ± 0.33)	5 (2.3 ± 0.67)
without Afterswarms	6	57 (9.5 ± 1.64)	12 (2.0 ± 0.82)	5 1 st -emerging VQs survived	45 (7.5 ± 1.84)	6 (1.0 ± 0.82)
EUROPEAN COLONIES						
E-NC-1 ^b	1	29	11	4 ^{th*} , 8 ^{th**}	18	9
E-NC-2 ^b	1	17	6	3 ^{rd*} , 6 ^{th**}	11	4
E-AZ-3 ^b	0	6	5	3 ^{rd**}	1	4
E-AZ-4 ^b	0	17	2	1 ^{st**}	15	1
E-AZ-5 ^b	0	9	1	1 ^{st**}	8	0
E-AZ-6 ^b	0	4	3	1 ^{st**}	1	2
E-AZ-7 ^b	0	6	1	1 ^{st**}	5	0
E-AZ-8 ^b	0	5	3	1 ^{st**}	2	2
E-AZ-9 ^b	0	5	1	1 ^{st**}	4	0
E-AZ-10 ^b	0	8	1	1 ^{st**}	7	0
E-AZ-11 ^b	0	4	2	1 ^{st**}	2	1
E-AZ-12 ^b	0	9	2	1 ^{st**}	7	1
Total (Mean±SE/colony)						
with Afterswarms	2	46 (23.0 ± 6.0)	17 (8.5 ± 2.50)	0 1 st -emerging VQs survived	29 (14.5 ± 3.50)	13 (6.5 ± 2.0)
without Afterswarms	10	73 (7.3 ± 1.23)	21 (2.1 ± 0.41)	9 1 st -emerging VQs survived	52 (5.2 ± 1.39)	11 (1.1 ± 0.44)

^a produced VQs in association with reproductive swarming; ^b produced VQs in association with experimental queen removal. * left colony with afterswarm; ** became new laying queen of colony.

her colony); (2) her fate (killed by a rival; survived to depart with an afterswarm or inherit the natal nest); (3) the number of rivals she eliminated through pre-emergence destruction and duels; and (4) her vibration rate (vibration signals received/30 min). The mean (± SE) vibration rate for VQs in the African colonies (65.4 ± 26.53) was almost ten times greater than the 6.8 ± 2.63 observed for the European colonies. To facilitate between-race comparisons, we standardized our data by calculating for each VQ a “relative vibration rate,” defined as her personal rate divided by the mean rate over all VQs within her colony (Schneider et al., 2001). The relative rates allowed us to assess if the same trends in signal use occurred in the African and European colonies that followed different reproductive strategies, regardless of the actual level of vibration activity observed. We present actual vibration rates in our figures to more precisely depict the levels of signaling activity recorded during the queen elimination periods.

For each colony, we determined its reproductive strategy (produced afterswarms or not) and the total duration of the rival elimination period (hours elapsing between the emergence of the first VQ until there was a sole survivor in the natal nest). Colonies

without afterswarms were categorized as multiple-VQ colonies (≥2 emerged VQs) or single-VQ colonies (1 emerged queen). All colonies with afterswarms were multiple-VQ colonies.

Statistical analysis: We examined the influence of colony reproductive strategy on the duration of the rival elimination period and overall levels of vibration activity using two-way ANOVA that had colony as the subject and generated a race-by-reproductive strategy interaction. We used two-way nested ANOVA (colonies nested within race) to compare the influence of reproductive strategy on the relative vibration rates experienced by surviving versus killed queens, and the relationship between VQ emergence order and relative vibration rate. The comparisons of vibration rates were restricted to the multiple-VQ colonies; the single-VQ colonies exhibited little vibration activity, all of which was focused on the sole emerged queen. Vibration rates were square-root transformed before analysis to achieve normality.

We used Kruskal-Wallis tests and log-linear models to examine the total number of queens involved in the replacement process and the number eliminated through duels versus pre-emergence destruction.

Contingency table Chi square analysis was used to examine the number of 1st-, 2nd-, 3rd-, etc. emerging VQs that survived the elimination process in colonies with and without afterswarms. When necessary, data were combined among cells within the contingency tables to ensure adequate sample sizes. The sequential Bonferroni adjustment was used to determine significance levels for the multiple comparisons made within and between races. All mean values are reported as \pm one SE.

Results

Of the 21 colonies used in the study, 16 did not produce afterswarms. Of these, eight were multiple-VQ and eight single-VQ colonies (Table 1). The remaining five colonies produced one afterswarm each. Two colonies produced afterswarms in conjunction with reproductive swarming, and three produced afterswarms in the process of replacing experimentally removed laying queens (Table 1).

We did not have afterswarming and non-afterswarming colonies of both races in each of the three study locations (Table 1). However, when viewed over all colonies in each area, we found no differences among the three locations for the number of queens produced per colony ($\chi_2^2 = 5.69$; $P = 0.06$), the duration of the elimination period ($F_{2,18} = 1.97$; $P = 0.17$), the vibration rates of emerged VQs ($F_{2,58} = 0.50$; $P = 0.61$), the association between vibration rate and VQ survival ($F_{2,55} = 1.32$; $P = 0.27$), or the association between vibration rate and VQ emergence order ($F_{9,39} = 1.43$; $P = 0.21$). Likewise, we also found no difference between colonies that produced afterswarms in association with reproductive swarming versus induced queen loss for any of the variables examined (for each ANOVA: $F_{1,3} < 2.16$; $P > 0.30$; for each Chi-square comparison: $\chi_1^2 < 5.2$; $P > 0.05$ with sequential Bonferroni adjustment). Thus, the basic trends in queen replacement were similar regardless of study area or the context in which afterswarming occurred.

Duration of replacement process, number of queens involved, and methods of elimination

The duration of the rival elimination period in colonies with afterswarms was about three times greater than that observed for colonies without afterswarms ($F_{1,17} = 12.76$; $P = 0.0023$; Fig. 1), and this trend was the same in both races ($F_{1,17} = 0.01$; $P = 0.941$). The colonies with afterswarms required 5–6 d to complete the queen replacement process, whereas those without afterswarms completed the process within 24–48 h.

The association between reproductive strategy and the number of VQs produced differed between the two races. African colonies with and without afterswarms produced a similar number of VQs ($\chi_1^2 = 1.74$, $P = 0.19$), whereas European colonies with afterswarms had more total queens than did those without afterswarms ($\chi_1^2 = 4.24$, $P = 0.0395$; Table 1). In both races, colonies

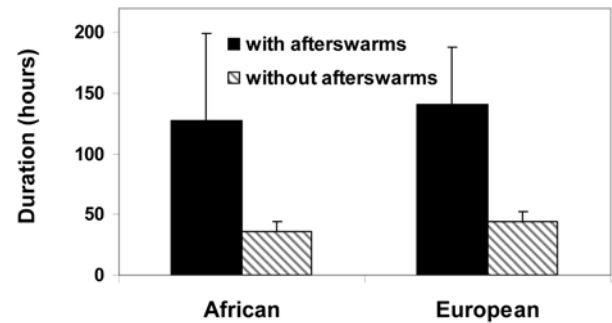


Figure 1. Mean \pm SE duration of the rival elimination period in the African and European colonies that did and did not produce afterswarms. Values above the columns indicate the number of colonies examined.

with afterswarms had more emerged VQs than did those without afterswarms ($\chi_1^2 = 6.59$, $P = 0.0102$; Table 1).

Colony reproductive strategy influenced the relative importance of duels versus pre-emergence destruction in the elimination process. Elimination through duels was more prevalent in colonies with afterswarms than without (Table 1), although the difference was not significant in either race ($\chi_1^2 = 0.20$, $P = 0.65$). The prevalence of pre-emergence destruction showed contrasting trends in the two races ($\chi_1^2 = 7.67$, $P = 0.0056$). In the African colonies, pre-emergence destruction was more pronounced when afterswarms were not produced, whereas in the European colonies it was observed more frequently when afterswarms occurred (Table 1).

Emergence order and VQ fate

The number of first-, second-, third-, etc., emerging queens that survived was significantly different in the colonies with and without afterswarms in both races ($\chi_2^2 = 12.59$; $P < 0.005$; Table 1). If afterswarms were not produced, 87.5% of the queens that survived to inherit the natal nest were the first VQs to emerge (Table 1). In the single-VQ colonies, the first queen to emerge eliminated all of her rivals through pre-emergence destruction. However, the first-queen advantage persisted even if multiple VQs emerged. In six of the eight non-afterswarming colonies that had more than one emerged queen, the first emerging VQ inherited the natal nest (Table 1). Thus, in colonies without afterswarms, the first emerged VQ had more opportunities to eliminate rivals through pre-emergence destruction, and may also have had an advantage in queen duels. In contrast, if afterswarms were produced, there was no first-queen advantage and early- and late-emerging VQs were similarly likely to survive in both races. In the colonies with afterswarms, only one first-emerging VQ survived to leave with an afterswarm, and none became the new laying queen of their natal nests (Table 1).

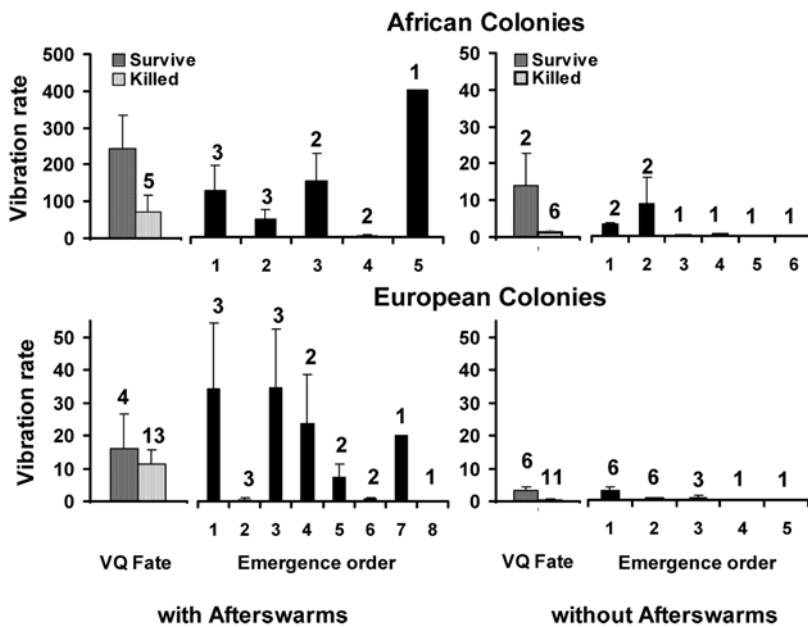


Figure 2. Mean \pm SE vibration rates experienced by surviving versus killed queens and by the 1st, 2nd, etc. VQs to emerge in the multiple-VQ African and European colonies with and without afterswarms. Values above the columns indicate the number of VQs examined.

Vibration signal activity

When viewed over all emerged VQs, the vibration rate in colonies with afterswarms (59.9 ± 21.9 signals/30 min) was almost 25 times greater than that observed in colonies without afterswarms (2.5 ± 0.73 signals/30 min; $F_{1,14} = 11.74$, $P = 0.0042$). This trend was exhibited by both races (Fig. 2), but was more pronounced in the African colonies, resulting in a significant race-by-reproductive strategy interaction ($F_{1,14} = 6.65$, $P = 0.022$).

When examining the emerged queens in multiple-VQ colonies, surviving queens were vibrated at higher rates relative to those that were killed ($F_{1,45} = 18.81$, $P < 0.0001$; Fig. 2). This trend was the same in colonies with and without afterswarms in both races ($F_{3,45} = 0.50$; $P = 0.685$; Fig. 2). Thus, the vibration signal was consistently associated with increased VQ success, regardless of the reproductive strategy or level of signaling activity exhibited by a colony.

Further evidence that the vibration signal was associated with queen success was provided by examining the relationship between a virgin queen’s emergence order and the rate at which she received signals in the multiple-VQ colonies. In colonies without afterswarms, vibration signals were concentrated almost entirely on early-emerging queens (Fig. 2), who were also more likely to survive the elimination process (Table 1). In contrast, in colonies with afterswarms, in which VQ survival was less associated with emergence order, all emerged VQs received some signaling activity regardless of emergence order (Fig. 2), resulting in a reproductive strategy X emergence order interaction ($F_{5,26} = 2.73$; $P = 0.0413$). These trends occurred similarly in the African and European colonies ($F_{9,26} = 0.89$; $P = 0.545$).

Discussion

The combined results from our studies suggest that colony reproductive strategy strongly influenced the dynamics of queen replacement. If a colony did not produce afterswarms, the queen replacement process was typically completed within less than two days, the first-emerging VQ usually inherited the natal nest even if multiple queens emerged, workers performed few vibration signals on emerged queens, and what little signaling activity occurred was directed entirely towards early emerging VQs. Other types of worker-queen interactions, such as chasing and biting, may also be reduced in colonies without afterswarms (Tarpy and Gilley, 2004; Gilley and Tarpy, 2005). In contrast, in colonies with afterswarms, the duration of the queen elimination process was three times longer, emerged VQs received vibration signals at much higher rates, there was no first-queen advantage, and a VQ’s emergence order did not strongly influence her success or the rate at which she was vibrated. The vibration signal was associated with increased VQ survival in both afterswarming and non-afterswarming colonies, and this may have occurred partly because the signal may allow workers to influence the timing and participants of queen duels (Schneider et al., 2001; Schneider and DeGrandi-Hoffman, 2003). Thus, in colonies with afterswarms, the greater use of the signal on VQs regardless of emergence order may have contributed to the survival of more queens and a longer replacement period. Worker chasing and biting of virgin queens also increase in colonies with afterswarms (Gilley, 2003; Tarpy and Gilley, 2004), which may further influence the timing of queen fights and extend the rival elimination period.

Taken together, these results suggest that worker behavior was the primary determinant for the outcome of

queen replacement. In colonies without afterswarms, queen replacement occurred with little worker interference, which may have allowed first-emerging VQs to quickly eliminate rivals. In contrast, when afterswarms were produced, workers may have influenced the ultimate fate of each emerged VQ through increased use of vibration signals and other interactions. Our results must be interpreted with caution, because we combined data from three studies conducted at different times and locations. However, we found no differences in the general trends for queen replacement among our three study sites, or among colonies that produced afterswarms under different conditions. Furthermore, the dynamics of queen replacement occurred similarly in our African and European colonies, despite the fact that the two races were not monitored in all environments. Thus, the associations that we observed between colony reproductive strategy and worker-queen interactions may be broadly applicable to queen-replacement decisions in honey bees over a wide range of conditions.

We did find differences between the African and European colonies with and without afterswarms in the total number of VQs produced and the relative importance of pre-emergence destruction in queen elimination. In comparison, Gilley and Tarpay (2005) found no difference between the races in the number of queens eliminated through pre-emergence destruction. The contrasts between our results and those of Gilley and Tarpay (2005) may arise from the relatively small number of afterswarming colonies examined in each study, as well as idiosyncratic differences among colonies within the two races. Nevertheless, these observations suggest that queen number and method of rival elimination may provide avenues for exploring differences in reproductive decision-making among honey bees adapted to different ecological conditions.

The patterns we observed for VQ activity and worker-queen interactions in our colonies with and without afterswarms may have been related to the potential for cooperation and conflict under different reproductive conditions (Visscher, 1993; Tarpay et al., 2004; Gilley and Tarpay, 2005). For example, if the vibration signal allows workers to influence VQ fights (Schneider et al., 2001; Schneider and DeGrandi-Hoffman, 2003), then the observed patterns of signal use may have reflected the degree to which worker interests were aligned with those of the queens. The low vibration activity directed only towards early-emerging VQs in the non-afterswarming colonies may have contributed to decreased worker interference and a rapid completion of the elimination process, and may have reflected a convergence of worker genetic interests with those of the first-emerging queen. In contrast, the higher vibration rates directed among multiple emerged VQs in colonies with afterswarms may have contributed to an extended elimination process and a reduced first-queen advantage, which may have reflected divergent interests of workers and VQs over the outcome of queen replacement in the natal nest. Worker

interactions that influence queen behavior may be shaped by selection acting at the level of the individual sterile worker, which may favor the preferential treatment of more closely related VQs, or at the level of the colony, which should favor interactions that promote the survival of better quality VQs regardless of relatedness (Gilley and Tarpay, 2005; Ratnieks et al., 2006). However, the factors affecting worker-queen interactions are unclear. There is no strong evidence for kin preferences during queen rearing (Breed et al., 1994; Visscher, 1998; Schneider and DeGrandi-Hoffman, 2002; Tarpay et al., 2004), worker-queen interactions (Tarpay and Fletcher, 1998; Gilley 2003; Chaline et al., 2004), or vibration signal performance (Lewis et al., 2002; Schneider and DeGrandi-Hoffman, 2003). Likewise, factors that may reflect VQ quality (size; weight; ovariole number) show no consistent influence on worker-queen interactions or queen survival (Tarpay et al., 2000; Gilley et al. 2003). Experiments that systematically alter queen relatedness and quality will be necessary to assess the relative roles of cooperation and conflict in formulating queen-replacement decisions in honey bee colonies following different reproductive strategies.

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