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ORIGINAL ARTICLE

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Evidence for genetic variation in worker task performance by African and European honey bees

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Abstract The dramatic competitive advantage of the African honey bee over European bees in the neotropics comes in large part from their faster rates of colony growth and reproduction. In honey bees, brood production, and thus colony growth, are controlled by the workers. Thus, we tested for genetic differences between African and European workers in their preference for tasks associated with brood production by monitoring individual African and European workers cross-fostered in common colony environments. We additionally examined differences in the age of transition between tasks (age polyethism). Our data provide strong evidence for genetically based differences in a subset of tasks. African workers were more likely to collect and process pollen, the nutrient source for brood. They initiated pollen foraging at a younger age, but this result was not significant after Bonferroni adjustment. African and European workers showed no difference in brood-care task performance, and did not vary in the age at which they performed brood-care tasks. These data suggest that a significant part of the competitive advantage of this major invasive pest can be traced to a small subset of worker behaviors, those involving resource intake.

Keywords Honey bee · *Apis mellifera ligustica* · *Apis mellifera scutellata* · Foraging behavior · Genetic differences

Introduction

Given the enormous economic and ecological impact of biological invasions, understanding what makes invasive species successful is of central importance. Most research on invasion species has focused on ecological, genetic, and life-history characteristics. However, the influences of behavioral mechanisms on invasion success remain virtually unknown (Holway and Suarez 1999). With the increasing movement of invasive species into new areas, it is becoming progressively more important to establish what role behavioral variation may play in their success.

The invasion by the African honey bee (*Apis mellifera scutellata*) into the neotropics and southwestern United States is a particularly dramatic example of biological invasion. The competitive advantage of African over established European honey bee populations (primarily *A. mellifera ligustica* and *A. mellifera mellifera*) is driven largely by their higher colony growth and reproductive rates (Otis 1980; Schneider and Blyther 1988; Winston 1980a, 1992; Winston et al. 1983), which in turn have a dramatic effect on population growth. African-derived honey bee populations moving into the neotropics have been reported to increase an estimated 16-fold per year (Otis 1980; Winston 1992). Maximal estimated increases in feral European colonies in temperate areas under mild temperature conditions are three- to sixfold (Winston 1980b).

The invasion of African bees into the neotropics has involved an almost complete replacement of local European bee populations, after some initial hybridization between the two subspecies (Hall 1990; Hall and Smith 1991; Smith et al. 1989). Because European bees have historically done poorly in tropical South America, it has been argued that the invasion of African bees cannot be viewed as a competitive replacement. However, in the last few years bees from tropical African-derived populations have essentially replaced feral populations in the southwestern United States, where European bees have traditionally been successful (Loper et al. 1999; Rinderer et al. 1993; Taylor and Spivak 1984). Because these bees have retained much of the genome of *A. m. scutellata*, we refer to them here as African or African-derived, rather than Africanized.

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Honey bees could theoretically compete reproductively via differences in male (drone) mating advantage, as well as through different colony growth and swarming rates. However, evidence for differences in mating success for the two subspecies is equivocal (Winston 1992). In contrast, there is strong evidence that African-derived bees out-compete European populations through higher rates of colony growth and swarming (Otis 1980; Schneider and Blyther 1988; Winston 1980a, b; Winston et al. 1983).

Colony-level differences affecting population growth of African and European bees have been well described. African colonies have higher brood production and associated higher pollen-intake rates (Danka et al. 1987; McNally and Schneider 1996; Pesante et al. 1987; Schneider 1989; Spivak 1992). Pollen is the primary nutrient source for developing brood, and variation in pollen-intake rates correlates positively with brood production (Eckert et al. 1994; Schneider and McNally 1992). In contrast, European bees have slower colony-growth rates, but maintain larger colony size by swarming less frequently. European colonies also store more honey than African colonies, aiding over-winter survival in temperate climates (Rinderer and Collins 1991; Schneider and Blyther 1988; Winston et al. 1981).

What are the mechanisms for these different colony-level strategies? In honey bees, brood production, and thus colony growth, are regulated primarily by the workers who rear the brood. We tested the hypothesis that African and European workers vary intrinsically in performance of tasks affecting brood production. Workers can influence brood production (and colony growth) in at least two ways. First, they could influence brood production directly via increased performance of brood-care tasks. Honey-bee workers perform a series of brood care behaviors, including feeding brood, capping cells as brood develop from larvae into pupae, and cleaning cells after brood emerge. Second, they could affect brood production indirectly via variation in preference for tasks associated with resource intake. Workers collect two resources relevant to brood production: nectar and pollen. While pollen is used specifically to feed developing brood, nectar functions as a general energy source for the colony, as well as a major ingredient in comb wax. Thus, variation in worker preference for pollen versus nectar collection could strongly influence colony brood production.

Honey-bee workers also perform a progression of different tasks as they age (age polyethism). In particular, workers generally perform in-hive tasks such as brood care at a younger age, and outside tasks such as foraging when they are older (Seeley 1982). Thus, it is additionally possible that African workers increase performance of key tasks associated with colony growth by beginning them earlier and performing them longer than European honey bees.

We also considered the hypothesis that variation in worker behavior is driven primarily by differences in African and European colony environments. Colonies vary in social interactions and resource cues. This variation could theoretically be more important in structuring social behavior than intrinsic (i.e. genetic) variation in worker task preference. For example, differences in worker brood care and foraging behavior could be driven by variation in queen egg-laying rates, and consequent effects on the amount of brood available for feeding. To evaluate these alternative hypotheses, we tested for intrinsic differences in the probability of performing tasks by African and European workers cross-fostered in common colony environments. We monitored workers in both African and European colonies to differentiate genetic from colony environment effects on behavior.

Methods

We placed newly emerged African-derived (*A. mellifera scutellata*) and European (*A. mellifera ligustica*) workers into common observation hives and monitored their behavior over approximately 4 weeks. Each worker was individually marked with a paint dot on the dorsum of the abdomen and a numbered plastic bee tag on the thorax. European workers came from managed colonies obtained from Allen's Bee Ranch, Redding, California. African workers came from the USDA African honey bee apiary near Tucson, Arizona.

All colonies at the USDA apiary were maintained as African stock. We confirmed that the colonies used in this experiment were African by mitochondrial DNA analyses (2 bees per colony) and allozyme electrophoresis for malate dehydrogenase (MDH-1; 20 bees per colony). All colonies had the African mtDNA haplotype (Hall and Smith 1991; Smith et al. 1989), and at least 80% of the MDH-1^{100} allele, the same frequency as reported for feral African colonies (Loper et al. 1999).

We performed two replicates of the experiment. In the first, we co-fostered African and European workers in two European host colonies. In the second, we co-fostered African and European workers in two European and two African host colonies. In both experiments we placed 300 individually marked 1- to 2-day old bees of African and European stock (600 total per colony) into each host colony. Host colony queens were unrelated to each other, and marked workers came from sources unrelated to the host colonies. Marked workers within each replicate were pooled from three African and three European source colonies, for a total of six African and six European source colonies across both experiments.

The host colonies were set up in observation hives 9 days before adding individually marked workers. Each hive contained 4 Langstroth frames, with Plexiglas walls on each side, marked with a 112-quadrat grid (36 cm^2 per quadrat) to help in locating individual bees. We gave colonies within each experiment similar amounts of honey, pollen, and brood. After adding the marked workers, we surveyed colonies and recorded the behaviors of marked bees every other day over 22 days in experiment 1 and 30 days in experiment 2.

Each hive was scan-sampled once in the morning and once in the afternoon, and the tasks performed by all observable marked bees were recorded. Observable tasks relating directly to brood production included feeding brood, capping brood that were beginning to pupate, and cleaning cells from which brood had recently emerged. In-hive tasks relating to resource intake included packing pollen into storage cells, and processing nectar (conversion of nectar into honey). We also recorded data for three general behaviors: cell inspection, walking, and inactivity.

We could not collect foraging data for the first experiment, because exterior nest entrances were not visible. In experiment 2, we observed the nest entrances during scan samples to determine when marked workers began foraging (days 12–13). Beginning on day 14, we observed hive entrances for 10 min after completing

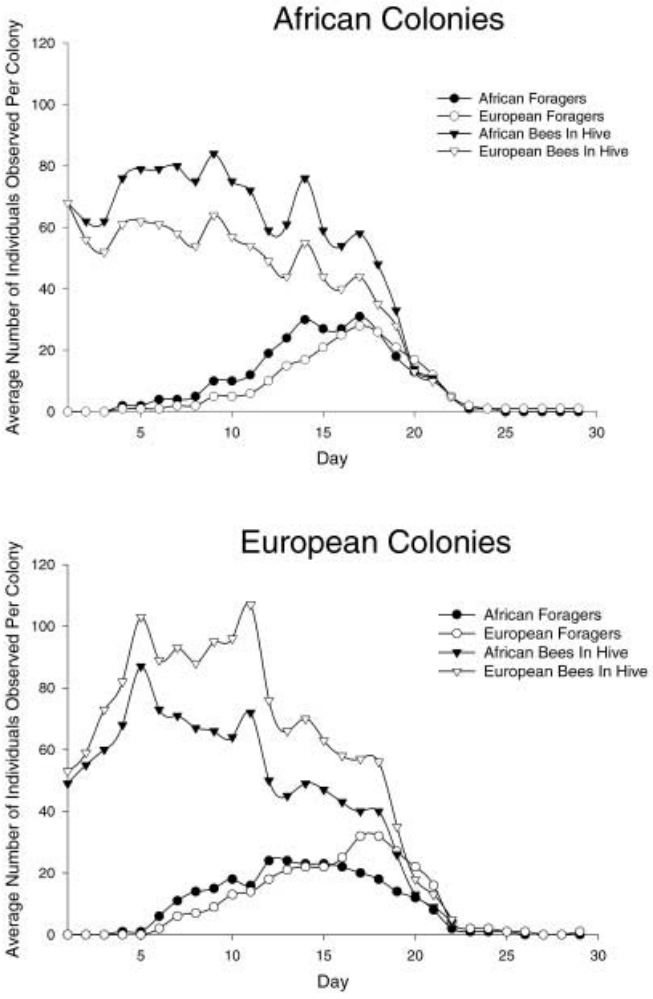

Fig. 1 The average number of African and European bees observed conducting in-hive and foraging tasks in African and European colonies each day (data are summarized and presented as 3-day running means)

each colony survey to monitor foragers. We identified workers as either pollen or non-pollen (primarily nectar) foragers, based on whether we observed pollen loads on their corbiculae. After day 23, almost all surviving marked bees were engaged in foraging (Fig. 1). At this time, we stopped in-hive observations, but continued to monitor hive entrances for two 10-min periods each day until day 30. By this time, almost all marked workers had died or disappeared.

Data were analyzed for genetic and colony-environment effects on: (1) the relative proportion of African or European workers performing a given task, (2) the age of task performance (first observed, mean age, last observed), and (3) the number of days that African or European workers were observed performing a task. We use the terms "genetic effects" and "colony-environment effects" with caution; our method of adding newly emerged workers into host colonies allowed us to tease apart the effects of the colony-environment on the adult worker bees from effects caused from differences generated collectively by genotype and possible larval environment effects or maternal effects. Thus, "colony-environment effects" should be considered the influence of the physical and social environment on adult worker-bee behaviors, while "genetic effects" include the influences of both genotype and maternal effects.

Differences in the proportion of African and European workers performing a given task were analyzed via χ^2 (genetic effects only; experiment 1) or log-linear analyses (maximum likelihood estimates, using the Newton-Raphson method, Systat 9.0; genetic and colony-environment effects; experiment 2). Because of the number of analyses, we Bonferroni-adjusted α values to $\alpha^1<0.007$ for experiment 1, and $\alpha^1<0.0056$ for experiment 2. The age of task performance was measured as: (1) the age that a worker was first seen performing a task, (2) the average age of workers performing a task, and (3) the age at which workers were last observed performing a task. Age data were analyzed via ANOVA and the α level was Bonferroni-adjusted to $\alpha^1<0.005$. The number of days between the first and last observed instance of performing an individual task were calculated for each worker, and then averaged among all African or European workers observed performing a given task one or more times. The α level was Bonferroni-adjusted to $\alpha^1<0.005$. We did not include workers that never performed a given task in these analyses. Because virtually all workers were observed until death, we did not apply survival corrections to the data.

Results

We observed 50–96% of all marked bees at least once in each colony. However, we analyzed data only for bees that were observed at least twice over the course of the experiment, 50–75% of all marked workers. An average ±SE (range) of 60±5.3 (8–158) African workers and 62±5.4 (13–140) European workers were observed per day performing in-hive tasks. This number declined as individuals began foraging (Fig. 1). Once foraging began, we observed 12±1.8 (0–52) African and 12±2.2 (0–93) European bees collecting resources each day. Observations were ended on day 29 when very few marked bees remained in any hive. (Fig. 1).

Genetic effects on task preference

African and European workers did not differ in their probability of performing virtually all tasks associated directly with brood care, including feeding brood and cleaning brood cells. There was one exception: capping brood was performed by a higher proportion of European than African workers in experiment 2 and showed a similar but non-significant pattern in experiment 1 (P=0.01, $a^1<0.007$; Tables 1, 2). However, this result is opposite to the expectation that an enhanced focus on brood care by workers produces the higher growth rates of African colonies. We also saw no significant difference between the two subspecies in the amount of time spent inactive, suggesting that overall activity levels for the two subspecies were the same (experiment 1: P=0.51; experiment 2: P=0.44).

In contrast, the two subspecies showed strong intrinsic differences in tasks associated with resource intake. African workers were significantly more likely to pack pollen than European workers in both experiments (Tables 1, 2). Conversely, European workers consistently showed a higher but non-significant probability of processing nectar in both experiments (Tables 1, 2; P=0.07 experiment 1; P=0.01 experiment 2; $a^1<0.005$)

An approximately equal proportion of African (62%) and European (61%) workers foraged in experiment 2,

Table 1 Percent of marked European and African workers seen performing different in-hive tasks in experiment 1. The χ^2 and *P* values indicate the probability that African and European workers were equally likely to be observed performing a task. Because of the number of analyses, the α level was Bonferroni-corrected to $\alpha^1<0.007$. The superscript ^{G} denotes behaviors for which African and European workers differed

	% Europeans (*N*=337)	% Africans (*N*=295)	Likelihood χ^2	*P* value
Direct brood production				
Feeding brood	53	52	0.02	0.88
Capping brood	24	16	7.1	0.01
Cell cleaning	45	39	0.43	0.51
General				
Cell inspection	78	78	0.001	0.98
Inactive	59	55	0.44	0.51
Resource intake				
Nectar processing	22	17	3.2	0.07
Pollen packing^G	12	24	16.1	<0.0001

Table 2 The percent of observed African and European workers performing in-hive and foraging tasks in experiment 2. Foraging tasks were additionally analyzed using only bees observed foraging. Data were pooled between colonies of a given genotype and were analyzed via log-linear for genotypic^G, colony environment^E and interaction^I effects. Because of multiple analyses, the α level was Bonferroni-corrected to $\alpha^1<0.0056$

Colony environment	European		African		Environment		Genotype		Interaction	
Genotype	European (*N*=456)	African (*N*=459)	European (*N*=363)	African (*N*=412)	χ^2	*P* value	χ^2	*P* value	χ^2	*P* value
Brood care tasks										
Feeding brood	46	40	43	41	0.02	0.884	4.38	0.0364	0.46	0.4958
Capping brood^G	14	4	6	5	1.99	0.1582	12.63	0.0004	0.95	0.3305
Cell cleaning	65	68	71	74	0.95	0.3305	3.79	0.0516	0.12	0.7334
Resource intake (% of all bees)										
Nectar Foraging^G	55	38	55	30	2.58	0.1083	76.41	<0.0001	1.15	0.2845
Reducing nectar^E	14	7	14	14	17.54	<0.0001	6.4	0.0114	0.4	0.5271
Pollen foraging^{G,E}	1	44	2	47	9.4	0.0022	307.74	<0.0001	2.74	0.0981
Pollen packing^{G,E,I}	12	32	21	28	9.7	0.0018	25.67	<0.0001	12.63	0.0004
General										
Cell inspection	32	37	32	33	1.36	0.2429	6.4	0.0114	0.12	0.7334
Inactive	36	41	34	43	0.15	0.6971	0.61	0.4363	1.25	0.2631
Resource intake (% of all foragers)	(*N*=273)	(*N*=248)	(*N*=226)	(*N*=289)						
Nectar foraging^{G,E}	98	69	97	43	11.77	0.0006	48.86	<0.0001	0.67	0.4133
Pollen foraging^G	3	40	3	64	1.3	0.2538	277.07	<0.0001	1.3	0.2538

but they differed dramatically in the resource they collected (Table 2). The vast majority (95%) of pollen foragers across all colonies were African. Conversely, a significantly higher proportion of European than African workers collected nectar; 64% of nectar foragers across all colonies were European. The position of the entrances did not allow us to reliably measure foraging behavior in experiment 1.

Colony-environment effects on task performance

We analyzed colony environment and environment X genotype interaction effects on the probability of task performance in experiment 2 (Table 2). More workers collected and packed pollen in African than in European colonies, although marked pollen foragers in European colonies were still almost exclusively African. There was additionally a significant interaction effect for packing pollen. Conversely, European colonies showed higher rates of nectar collection and reducing nectar than African colonies.

Genetic effects on age polyethism

African and European workers moved through in-hive tasks at similar rates. They did not differ significantly in the age first or last observed performing in-hive tasks, and in average age of task performance (Fig. 2, Table 3). Further, the total number of days that bees performed individual in-hive tasks did not differ significantly between the subspecies (all age data analyzed via 2-way ANOVA for colony environment and genetic effects; Fig. 2).

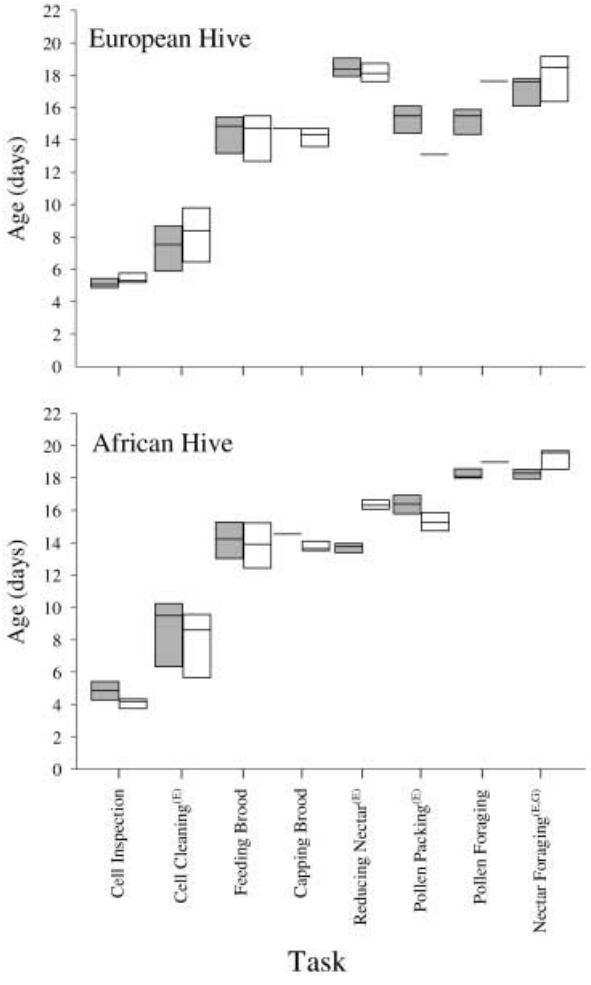

Fig. 2 The age at which African and European workers performed tasks in African and European colonies. The *bottom* and *top* of the *vertical bars* show the average age workers were first and last observed performing the task, respectively. The average age workers were observed performing the task is represented by the *horizontal line* extending through the *bar*. In the case where all individuals were observed performing the task only one time, the *horizontal line* represents the average age. Statistically significant differences between African versus European workers and African versus European colonies are shown as superscript (*G*) and (*E*), respectively, and exact *P* values are presented in the text. Because ten ANOVA statistics were run, the α level was Bonferroni-adjusted to $\alpha^1<0.005$. Standard errors and sample sizes are given in Table 3

African bees generally initiated foraging at an earlier age (P=0.001; Table 3) and were last observed foraging at a younger age than European foragers (P<0.001; Fig. 2). Because of this, African and European workers actually spent the same total number of days foraging (P=0.397). We also analyzed foraging age separately for nectar and pollen foragers. African and European nectar foragers initiated foraging at almost identical ages (P=0.148). Although European nectar foragers ended performance of this task at a slightly later age (P<0.001), this did not generate a significant difference in the total days spent nectar foraging (P=0.406; Fig. 2). African workers collected pollen at a younger age than European workers, but the result was not significant. African workers initiated pollen collection slightly earlier (P=0.019; Table 3), and foraged for a slightly longer total period (1.5–2 days more, P=0.03).

Colony-environment effects on age polyethism

Colony environment had a significant effect on task ontogeny for both in-hive tasks and foraging. However, it did not influence performance of in-hive tasks in a consistent way (Fig. 2). Workers began and ceased to reduce nectar significantly earlier in African colonies. Conversely, the average age at which workers were observed cell cleaning was younger in European colonies than in African colonies (P<0.001; Fig. 2).

Colony environment also influenced foraging age (Fig. 2; Table 3). Age of first foraging, average foraging age and age last seen foraging were earlier for workers in European colonies (P<0.001 for each measure). However, the total time spent foraging did not differ between colony types (P=0.31). Colony environment influenced both pollen and nectar collection in a similar manner (Fig. 2). Workers in European colonies initiated nectar foraging approximately 2 days earlier (P<0.001), and had a significantly lower mean age observed foraging (P<0.001). Pollen foragers showed a similar but non-significant result in which they initiated foraging approximately 2.5 days earlier in European colonies (P=0.006). The average age that pollen foraging was observed in European colonies was also significantly lower than in African colonies (2.1 days; P=0.005).

Although there was no significant effect of colony environment on the last day seen foraging, this measure was earlier in European colonies for both pollen and nectar collection (P=0.025 and P=0.008, respectively; Tables 1, 2; Fig. 2). Consequently, the total number of days that individual foragers collected pollen and nectar did not differ between the African and European colony environments (pollen: P=0.636; nectar: P=0.082).

Discussion

Behavioral characteristics responsible for invasion success

In this study, we asked whether African and European workers varied intrinsically in a suite of behavioral characteristics with the potential to influence colony growth rate. Our data suggest that they differ significantly only in a limited number of key behaviors, those related to resource intake. African workers showed consistently higher intrinsic preferences for pollen-related tasks than European workers. Rates of pollen foraging and processing were additionally higher for both subspecies when reared in African colonies, suggesting that the African colony environment provides a stronger stimulus for pollen collection. Conversely, European workers showed a preference for nectar collection, and rates of nectar pro-

Table 3 Comparison of average age first observed performing tasks between African and European honey bees cross-fostered in African and European colonies. Sample size and standard error are contained in *parentheses*. Analysis indicates whether colony environment, genotype, and/or the interaction between the two influence age. Because ten ANOVA statistics were run, the α level was Bonferroni-adjusted to $\alpha^1<0.005$

Colony environment	African		European		Environment		Genotype		Interaction	
Genotype	African	European	African	European	*F*-ratio	*P*	*F*-ratio	*P*	*F*-ratio	*P*
Capping brood	14.5 (20, 1.04)	13.6 (22, 1.44)	14.7 (32, 1.01)	14.2 (78, 0.46)	0.198	0.657	0.524	0.47	0.024	0.877
Cell cleaning	6.4 (272, 0.31)	5.9 (256, 0.33)	5.9 (255, 0.25)	6.4 (293, 0.22)	0.029	0.866	0.007	0.934	3.339	0.066
Cell inspection	4.6 (134, 0.39)	3.8 (116, 0.37)	5 (122, 0.30)	5.2 (125, 0.36)	6.539	0.011	0.798	0.372	1.983	0.16
Feeding brood	13 (159, 0.43)	12.4 (157, 0.43)	13.6 (200, 0.32)	12.8 (258, 0.27)	1.98	0.16	3.425	0.065	0.098	0.755
Reducing nectar^{H}	13.3 (85, 0.58)	16.1 (60, 0.75)	18.2 (25, 0.84)	17.9 (61, 0.43)	21.858	<0.001	2.986	0.085	4.363	0.038
Pollen packing	15.7 (116, 0.42)	14.8 (77, 0.55)	14.7 (62, 0.46)	13.1 (15, 1.20)	3.554	0.06	3.008	0.084	0.143	0.706
Nectar foraging^{H}	18 (113, 0.35)	18.5 (180, 0.23)	16.3 (139, 0.32)	16.5 (186, 0.26)	40.506	<0.001	2.094	0.148	0.327	0.567
Pollen foraging	18 (164, 0.22)	19 (7, 1.56)	14.5 (89, 0.38)	17.6 (7, 1.53)	7.733	0.006	5.056	0.019	1.346	0.247
All in-hive tasks^{H,I}	5.9 (410, 0.25)	4.5 (338, 0.24)	5.8 (371, 0.21)	6.3 (422, 0.20)	17.095	<0.001	2.691	0.101	15.371	<0.001
Foraging^{H,G}	18 (290, 0.20)	18.9 (226, 0.20)	15.9 (248, 0.24)	17.3 (273, 0.21)	71.725	<0.001	26.688	<0.001	1.051	0.306

cessing and nectar foraging by both subspecies were higher in the European colony environment.

Our data on worker-level differences in foraging fit well with information on variation in colony-level foraging strategy between the two subspecies. African colonies have higher pollen-intake rates (Danka et al. 1987; Pesante et al. 1987; Schneider 1989; Schneider and McNally 1992). However, African and European colonies in the neotropics store pollen at similar levels, suggesting that the higher levels of pollen entering African colonies are converted to brood (Spivak 1992). In contrast, European colonies generally store more honey than African colonies (Rinderer and Collins 1991; Schneider and Blyther 1988; Winston et al. 1981).

African and European colonies also differ in brood production; the proportion of comb-containing brood is generally 2–4 times higher in African colonies (Schneider and Blyther 1988; Winston 1992). Despite this, we found no consistent differences between African and European workers in any of the measured brood-care activities. However, we did find colony-environmental effects on brood care, suggesting that both African and European workers are highly sensitive to the social cues eliciting brood care. These data suggest a model in which intrinsic variation in worker resource preference generates differences in the colony's ability to support developing brood. This in turn produces a stronger stimulus environment for brood care. Thus, the apparent genetic effects on one suite of behaviors can have cascading effects on the social environment, the behavior of other workers, and consequent colony growth.

Genetic effects on worker behavior

Our data are the first demonstration of what appear to be genetic differences between African and European workers for foraging-task preference. Because we could not control for differences in larval nutrition, a component of this difference could be due to environment. However, our data are consistent with known genetic effects on foraging in European bees. Worker preferences for pollen or nectar collection within European populations are correlated with genotypic variation (Calderone and Page 1988; Fewell and Page 1993; Page and Robinson 1991). Furthermore, selection for differences in pollen hoarding at the colony level produces workers that vary in preference for both pollen and nectar collection (Fewell and Page 2000; Page and Fondrk 1995). Genomic studies have additionally connected variation in preference for pollen versus nectar in European bees to specific quantitative trait loci (Hunt et al. 1995).

Our data also provide the first detailed look at the age polyethism schedule for African-derived bees. African and European workers showed almost identical age trajectories for in-hive tasks (Fig. 2). However, we found weak but significant genetic effects on foraging ontogeny. Because we observed colonies until all but a small number (<5) remained in the hive, our data bracket the entire lifespan for each worker. African workers began foraging approximately 1 day before European workers. Because African workers also ended foraging earlier, total foraging lifespans did not differ between subspecies. Additionally, most of the measured variation in foraging

age was generated by pollen foragers; African workers had both a higher propensity for pollen foraging and initiated foraging slightly earlier. This finding is consistent with that of Pankiw and Page (2001), who report that an earlier age of transition to foraging is genetically correlated with an increased preference for pollen (versus nectar) collection in selected lines of European bees.

We found an effect of rearing environment on the age at which workers initiated both pollen and nectar collection, indicating that environment plays a strong role in the transition from in-hive tasks to foraging. Winston and Katz (1982) also found colony-environment effects on age of first foraging in co-fostered African and European bees. Our earliest age of first foraging was by African pollen foragers in European colonies. In their study, it was by European workers in African colony environments. These results at first seem contradictory. However, if the European workers in the Winston and Katz study were primarily collecting nectar (which is likely), they may indicate parallel mechanisms. In both cases, the genotype with a higher proclivity for performing a given task began performing that task earlier in a colony environment where the task was being performed at generally lower levels.

An earlier transition to foraging for African bees has also been reported by Giray et al. (2000). They examined the foraging ages of the first 50 precocious foragers in colonies of same-aged bees, and found that African workers clustered earlier in this group. Workers in these colonies tend to forage much earlier than those in colonies with more normally distributed age groups. Additionally, foragers were not identified as pollen or nectar collectors, making it difficult to compare foraging ages directly between studies. Although genetic effects on foraging age are apparent throughout these multiple studies, the effects are often weak relative to environmental effects. These data collectively suggest that differences in foraging age between African and European workers are unlikely to be a primary explanation for the large differences in colony-resource intake strategy between the two subspecies.

Selection on life-history strategy in African and European bees

What selective factors might drive the apparent genotypic differences in worker-task preferences between African and European bees? Life-history theory emphasizes there are trade-offs between allocation to somatic growth and to reproduction, and that the fitness consequences vary across environments (Clutton-Brock 1988; Stearns 1992). In honey bees, as in other social insects, allocation to colony growth and swarming is a trade-off between survival and reproductive costs (Bourke and Franks 1995; Müller and Schmid-Hempel 1992).

Species should have lower investment in reproduction relative to somatic growth in environments when there is a predictable negative relationship between size and mortality (Bourke and Franks 1995; Clutton-Brock 1988). The European traits of larger adult colony size, slow colony growth, and lower swarming rates have been likened to those of a "*K*"-selected strategy on the *r*/*K* continuum (Seeley 1978). European honey bees in temperate climates experience predictable mortality rates in winter, which are affected by energy (honey) stores and colony size (Seeley and Visscher 1985). These forces have likely resulted in increased fitness of colonies that swarm less frequently, and which have large honey stores.

In contrast, mortality for African colonies in their native environment occurs primarily from highly unpredictable events, including resource dearths and predation (Schneider and Blyther 1988; Schneider and McNally 1992). These conditions are associated with a more *r*-selected strategy (Bourke and Franks 1995), and may have resulted in increased fitness for colonies with the fastest colonial growth and reproductive rates. This in turn caused increased selection for individual worker preference for pollen versus nectar foraging, behaviors that are genetically variable, and which have a strong impact on colony-brood production. Our data suggest one mechanism by which selection acts on these traits is via worker resource choice. Thus, a significant part of the competitive advantage of this invasion population may be traceable, not to a suite of characters, but to differences in a small subset of worker behaviors.

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