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# Genetic determination of nectar foraging, pollen foraging, and nest-site scouting in honey bee colonies

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**Summary.** Allozyme analyses of honey bee workers revealed significant differences in the intracolonial subfamily composition of groups of nectar foragers, pollen foragers, and nest-site scouts. These differences demonstrate that colony genetic structure influences the division of labor among older foraging-age bees just as it does for younger workers. The maintenance of genetic variability for the behavior of individual workers and its possible effects on the organization of colonies are discussed.

## Introduction

Division of labor among workers is fundamental to the organization of complex insect societies. It is proposed to be more efficient for colonies to accomplish tasks with ensembles of specialized individuals than with undifferentiated workers (Oster and Wilson 1978; Wilson 1985, 1987). Understanding the evolution and mechanisms of division of labor are thus important objectives in the study of social behavior. Worker differentiation is assumed to be a product of colony-level selection (Oster and Wilson 1978), but the underlying genetic mechanisms have received relatively little attention (Crozier and Consul 1976; Owen 1986). Consequently, the proximal determinants of division of labor among workers in insect colonies are thought to be primarily, if not exclusively, environmental and ontogenetic (Wilson 1985).

A new perspective on division of labor is beginning to emerge from studies of *Apis mellifera* (Calderone and Page 1988; Frumhoff and Baker 1988; Robinson and Page 1988a, 1988b). It is concordant with a Darwinian model proposing that colony-level selection can change the distribution of workers with certain traits in colonies of a population (Darwin 1962, pp. 253–254; see Page et al. 1988). Calderone and Page (1988) demonstrated genotypic differences in the tendency to specialize on pollen foraging between workers from artificially selected strains (Hellmich et al. 1985) that were co-fostered in wild-type colonies. Frumhoff and Baker (1988) and Robinson and Page (1988a) reported that the genetic structure of honey bee colonies affects the division of labor. Polyandrous mating (reviewed by Page 1986) and simultaneous use of sperm from at least several drones (Page and Metcalf 1982; Laidlaw and Page 1984) results in colonies composed of numerous subfamilies (Laidlaw 1974). Each subfamily is a group of workers descended from the queen and one of her mates. Subfamilies often differ in their likelihood of guarding the nest entrance, removing dead bees from the nest (Robinson and Page 1988a), and grooming nestmates (Frumhoff and Baker 1988). These findings demonstrate genetic differences in worker behavior within colonies, the first requirement of Darwin's model for the evolution of worker castes. The results of Calderone and Page (1988) were a consequence of artificial colony selection (Hellmich et al. 1985). They demonstrate by analogy that colony-level selection can affect the genotypic composition of workers within colonies and result in differences in colony performance, satisfying the second and third requirements of the Darwinian model.

The extent to which colony genetic structure influences the divison of labor among workers is not known because only a few tasks have been examined thus far. Here we present evidence for subfamily differences in honey bee nectar foraging, pollen foraging, and scouting for new nest sites.

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Data come from ten colonies, including the five used for investigations of guarding and undertaking previously reported (Robinson and Page 1988a). Foraging and scouting are normally performed by workers older than guards and undertakers, usually greater than 20 days of age (reviewed by Nowogrodzki 1984; Seeley 1985; Winston 1987). Scouting, like guarding and undertaking, is a rare task, performed by ca. 5% of a swarm's population during the colony fissioning process (Seeley et al. 1979), while foraging is thought to be one of the more common activities in a honey bee colony (Sekiguchi and Sakagami 1966).

## Methods

Bees performing a task ("task performers") were collected from colonies composed of subfamilies with distinct allozyme markers. After identifying subfamily membership with polyacrylamide gel electrophoresis, we determined whether there were differences between the subfamily composition of samples of nectar foragers and pollen foragers and between nest-site scouts and other bees in swarms. A total of 3381 individuals were analyzed.

### *Colonies with allozyme markers*

Three unrelated queens (*Apis mellifera*) were selected to be mothers of 10 virgin queens and 8 additional unrelated queens were selected to be mothers of haploid drones. Each virgin queen was instrumentally inseminated (Laidlaw 1977) with the semen of 3 unrelated drones. Each drone carried a different allozyme of *malate dehydrogenase-1* (*Mdh*), designated "slow" (S), "medium" (M), and "fast" (F) (Contel et al. 1977). Semen from each drone trio was pooled, diluted, and homogenized to help stabilize the relative frequencies of different subfamilies over time (Kaftanoglu and Peng 1980; Moritz 1983).

Four of 10 inseminated queens were homozygous at the *Mdh* locus (SS: Colonies 4438, 4440, and 4456; MM: Colony 4453) and produced worker progeny with 3 distinct allozyme phenotypes that corresponded to 3 subfamilies. Five queens (Colonies 4439, 4442, 4445, 4450, and 4464) were SF heterozygotes; their offspring also belonged to 3 subfamilies but displayed 5 allozyme phenotypes: SS, SM, SF, MF, and FF. To simplify data analysis and presentation, workers sampled from colonies headed by the 3 heterozygous queens were grouped into 3 subfamilies as follows: SM and MF bees belonged to the M subfamily because the M allele only could be paternally inherited. SF bees were assigned to the S and F subfamilies in direct proportion to the ratio of SS to FF bees in each sample, because the maternal S and F alleles segregate in a 1:1 ratio. Subfamily membership was determined similarly for individuals from Colony 4457, derived from a SM queen.

*Mdh* allozymes are reliable biochemical markers. *Mdh* alleles segregate in Mendelian fashion and the electrophoretic mobilities of the allozymes they code for are known for all honey bee life stages (Contel et al. 1977; Nunamaker and Wilson 1980; Del Lama et al. 1985). In addition, using allozymes as genetic markers enabled behavioral determinations to be made blindly, with no prior knowledge of subfamily affiliation.

### *Behavioral classification*

When possible, 40 appropriately identified individuals were collected for each task from each experimental colony. Samples of foragers were collected twice from each colony, at 6–8 day intervals. Scout samples were collected from artificial swarms from 5 colonies; one swarm was established and one sample of scouts collected from each of 4 colonies, and 2 swarms were sampled from one colony. Workers were classified by task, as follows, and then collected and stored at −70° C for electrophoresis.

*Nectar foragers.* Bees returning to the colony alighted on a piece of 8-mesh hardware cloth (44.5 × 61.0 cm) that temporarily obstructed the hive entrance. Foragers, initially identified by their distended abdomens, were individually collected in cylindrical screen cages (10 cm long × 2 cm diameter) and anesthetized with $CO_2$. Measurements of expressed foregut contents were made to confirm foraging status (Gary and Lorenzen 1976); only bees with foregut load volumes >10 µl were classified as foragers. This standard clearly differentiated returning foragers from outgoing bees because the foregut load volume for workers leaving a colony is ca. 1µl (Gary and Lorenzen 1976). Foregut loads were analyzed with a refractometer to distinguish nectar collectors from water collectors. Again, the 2 groups were unambiguous: the sugar concentration in foregut loads was either less than 5%, indicating a water forager (Lindauer 1955a), or greater than 25% (nectar forager).

*Pollen foragers.* Workers observed on the entrance screen (described above) with pollen loads in their corbiculae were collected with a portable vacuum cleaner. Foregut contents were not assayed, so it is not known whether some pollen foragers also collected nectar.

*Scouts.* Artificial swarms were prepared (Morse 1961) 3 weeks to 4 months after foraging samples were obtained. A portion of a colony's workers was shaken from combs into a wooden cage (15 × 25 × 25 cm) with wire mesh sides. The colony's queen was confined in a smaller cage and suspended in the cage with the workers. Bees in the cage were fed 50% sugar syrup *ad libitum* for ca. 18 h to induce swarm-like behavior. The following morning the caged queen and a 1 L jar of sugar syrup were attached to a metal cross anchored in the ground and the caged bees dumped at the foot of the cross. The bees clustered around the queen and within 6 h were observed performing recruitment dances, presumably for potential nest sites that are typical of natural swarms (Lindauer 1955b; Seeley et al. 1979). Dancing bees were classified as scouts and collected over a 2–4 h period until 40 were obtained or until no new scouts were observed for 1 h. As a comparison group, immediately after collecting scouts we sampled bees from swarm clusters that were not dancing or following dancers ("non-dancers") at the time of their collection.

### *Stability of colony genetic structure*

The efficacy of the method used to mix semen was assessed by collecting samples of 6–8-day-old worker larvae and prepupae from each experimental colony. Three collections were made at 7–8 day intervals, beginning 2 weeks before the first forager samples were taken. Subfamily frequencies were determined by electrophoresis, as above.

## Results

Subfamily frequencies in 3 samples of worker larvae and prepupae taken at 7–8 day intervals did

**Table 1.** Stability of colony genetic structure in honey bee colonies composed of electrophoretically distinguishable subfamilies. Frequencies of individuals belonging to each subfamily are compared in 3 samples of worker larvae and prepupae ($n=34$–51) taken at 7–8 day intervals. Probabilities based on G-tests for heterogeneity (Sokal and Rohlf 1981)

| | Colony | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 4438 | | | 4439 | | | 4440 | | | 4442 | | | 4445 | | |
| Subfamily | S | M | F | S | M | F | S | M | F | S | M | F | S | M | F |
| Sample 1 | 21 | 5 | 23 | 17 | 10 | 13 | 13 | 14 | 23 | 17 | 14 | 9 | 2 | 36 | 12 |
| Sample 2 | 18 | 12 | 20 | 16 | 12 | 12 | 13 | 16 | 12 | 14 | 15 | 11 | 3 | 25 | 22 |
| Sample 3 | 12 | 5 | 22 | 12 | 14 | 14 | 19 | 9 | 12 | 18 | 20 | 2 | 11 | 21 | 9 |
| | $P>0.25$ | | | $P>0.75$ | | | $P>0.1$ | | | $P>0.05$ | | | $P<0.01$ | | |
| | Colony | | | | | | | | | | | | | | |
| | 4450 | | | 4453 | | | 4456 | | | 4457 | | | 4464 | | |
| Subfamily | S | M | F | S | M | F | S | M | F | S | M | F | S | M | F |
| Sample 1 | 0 | 16 | 24 | 17 | 10 | 13 | 18 | 10 | 21 | 11 | 19 | 10 | 2 | 14 | 24 |
| Sample 2 | 5 | 23 | 12 | 17 | 10 | 13 | 18 | 15 | 18 | 11 | 19 | 10 | 1 | 12 | 27 |
| Sample 3 | 0 | 16 | 24 | 13 | 16 | 11 | 14 | 11 | 15 | 6 | 23 | 11 | 0 | 12 | 22 |
| | $P<0.01$ | | | $P>0.5$ | | | $P>0.75$ | | | $P>0.5$ | | | $P>0.5$ | | |

not change significantly for 8 of 10 colonies (Table 1). In contrast, significant differences between the subfamily composition of samples of pollen foragers and nectar foragers were detected in 9 of 10 colonies at least once (12 of 20 trials; 10 colonies, 2 trials each) (Fig. 1). The subfamily composition of samples of scouts and non-dancers differed significantly for 3 of 5 colonies (3 of 6 trials) (Fig. 2).

These results were assessed with an experimentwise test. We used binomial tests to calculate the probability of getting as many or more significant trials as we report due to chance alone. For both foraging and scouting the number of trials that showed a significant deviation ($P<0.05$) was greater than that expected due to chance alone ($P<0.001$; based on the assumption of independence for the trials from each colony).

Subfamily frequencies for scouts and non-dancers did not change significantly ($P>0.05$) from trial to trial for the one colony (4445) that provided 2 swarms, despite a 7-week interval between their establishment. Environmental influences on the probability of task performance are suggested by differences between trials in the subfamily structure of some samples of nectar and pollen foragers (Fig. 1). Perhaps these are attributable to genotypic differences in the response to changing resource availability and/or colony needs.

## Discussion

Our results demonstrate that colony genetic structure is an important determinant of task specialization for older bees, just as it is for middle-aged workers (i.e., guards and undertakers; see Robinson and Page 1988a). Differences in nectar and pollen foraging imply that subfamilies can vary not only in the probability of performing rare tasks (Frumhoff and Baker 1988; Robinson and Page 1988a), but also in the manner in which they perform a common activity such as foraging.

These results also provide additional evidence for a genetic component to inter-individual behavioral variation in honey bees (see also Frumhoff and Baker 1988; Robinson and Page 1988a). The occurrence of workers that engage in tasks that are not performed by most colony members, like guarding (Moore et al. 1987), removing corpses (Visscher 1983), and scouting (Seeley et al. 1979), is one of the most intriguing forms of division of labor in insect societies (Oster and Wilson 1978). For example, scout bees, although only a small fraction of the swarm population, play a pivotal role in the reproductive process of colony fissioning; they scout for potential nest sites and then direct the entire swarm to the new location (Seeley et al. 1979). Previous studies have shown that scouting behavior cannot be explained by age polyethism alone. Nest-site scouts tend to be forag-

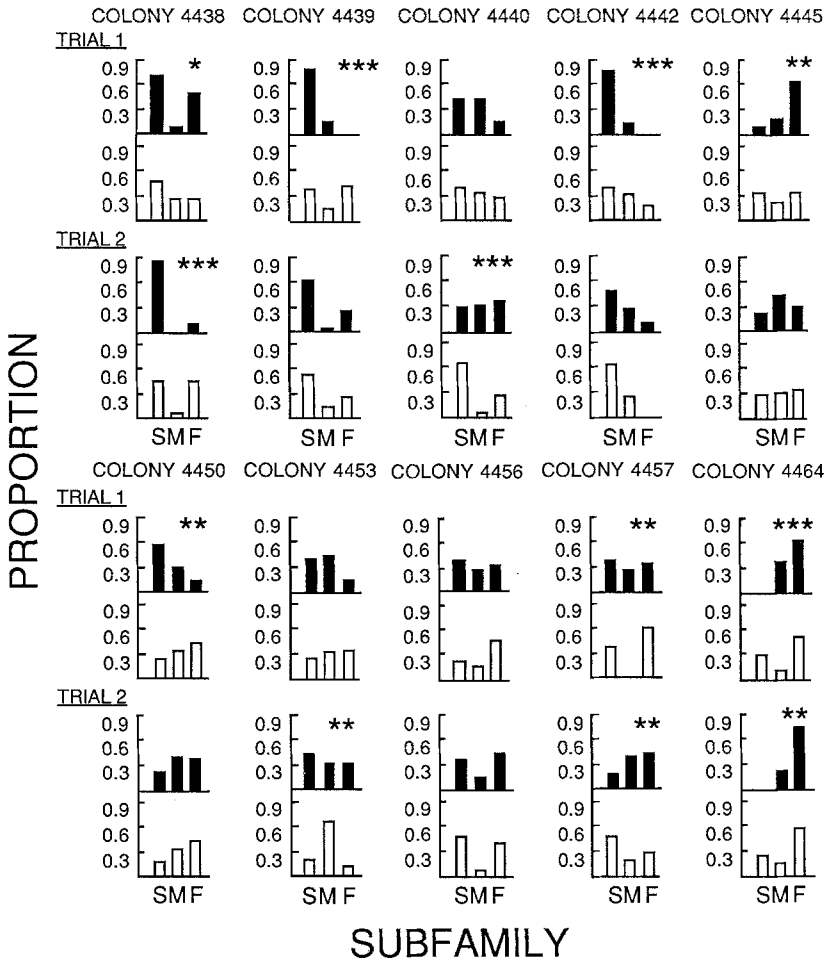


**Fig. 1.** Genotypic composition of samples of pollen foragers (■) and nectar foragers (□) from honey bee colonies composed of electrophoretically distinguishable subfamilies. Statistical analyses: * $P<0.05$; ** $P<0.01$; *** $P<0.001$, based on G-tests of actual frequencies ($n=38$–40). Intertrial differences for nectar foragers: Colonies 4440, 4442, 4453, and 4457: $P<0.01$; for pollen foragers: Colony 4439: $P<0.001$, Colonies 4442, 4445, and 4450: $P<0.01$

ing-age bees (Lindauer 1955b) but do not constitute a distinct age group relative to other older, non-scouting individuals. Similarly, differences in age and experience do not completely account for differences between food scouts and recruits (Oettingen-Spielberg 1949; Lindauer 1952), though Seeley (1983) suggested that a relatively higher proportion of food scouts are older foragers. We found that half the samples of nest-site scouts were genotypically different from samples of non-dancers representing the composition of the entire swarm. However, because scouts are among a swarm's older individuals (Lindauer 1955b) while our swarms probably consisted of bees of all ages, the observed differences could be a consequence of non-random patterns of sperm use coupled with age polyethism. We attempted to minimize this potential problem by using semen from drones that was pooled, diluted, and homogenized for inseminations. This technique has been shown to mix sperm of different males (Moritz 1983). Larval samples taken from our experimental colonies several months prior to the establishment of artificial swarms suggest that the relative frequencies of different subfamilies were adequately stable over time. However, because the time period encompassed by these samples does not correspond to the times at which scouts were collected, more detailed studies are needed to verify the subfamily differences in scouting behavior reported here.

It is unlikely that the observed subfamily differences in foraging behavior are a consequence of non-random patterns of sperm usage coupled with age polyethism. Among foraging-age bees, the probability of collecting either nectar or pollen is not age-dependent (reviewed by Free 1965; see also Sekiguchi and Sakagami 1966), and we compared nectar foragers directly with pollen foragers collected at the same time. Subfamily differences in foraging are consistent with a previous report suggesting genetic variation in the foraging behavior of workers from different colonies (Free and Wil-

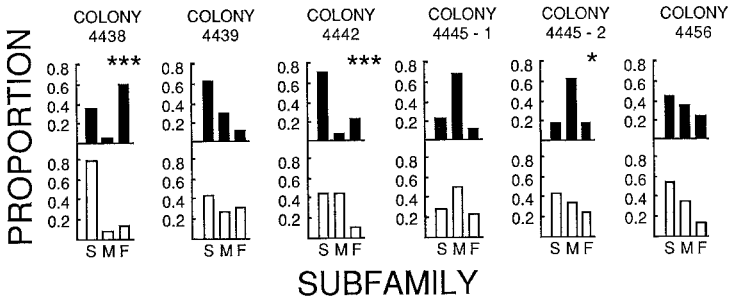


**Fig. 2.** Genotypic composition of samples of scouts (■) and non-dancers (□) from artificial swarms of honey bees composed of electrophoretically distinguishable subfamilies. Statistical analyses as in Fig. 1 ($n = 36$–40). Two swarms were established from Colony 4445

liams 1973). They also confirm earlier findings with artifically selected strains of bees (Calderone and Page 1988).

Intracolonial genetic variation in worker task performance may influence the ergonomic organization of colonies. The "phenotype" of a colony for any given behavioral trait may be at least partially determined by the composition and behavior of its subfamilies (Robinson and Page 1988a, 1988b). Under standard assumptions of quantitative genetic models (Falconer 1981), additive effects of all subfamilies may define the colony phenotype for some tasks, particularly those involving large numbers of workers. For more rare tasks, such as guarding, undertaking, and scouting, performed by only a fraction of a colony's workers, there may be non-additive effects of "behavioral dominance" (Craig 1980) by individuals of only a few subfamilies on the colonial phenotype. That is, a worker genotype that results in an extremely low response threshold for a task may strongly influence the colony's performance of that task even if possessed by a minority of a colony's workers. As a consequence of behavioral dominance, the performance of a rare task by a colony with only a small number of workers possessing extremely low response thresholds may be similar to that of a colony with a larger proportion of such workers. For a rare task, the actions of a relatively small number of bees can generally satisfy colony needs and maintain the stimulus level below the response thresholds of less sensitive individuals via a negative feedback loop of task regulation. We suggest that greater genetic variation exists for rare tasks than for common tasks because behavioral dominance may mask the effects of the other subfamilies' behavior on the colony phenotype, thus minimizing their exposure to colony-level selection. This hypothesis is consistent with the findings of Frumhoff and Baker (1988), who reported subfamily differences for allogrooming, a rare activity, but no differences for trophallaxis, performed by a larger number of workers.

Our results, together with those of Calderone and Page (1988), Frumhoff and Baker (1988), and Robinson and Page (1988a) support Darwin's model for the evolution of division of labor and demonstrate that colony-level selection can change worker behavior by acting on the genotypes of workers rather than of queens. Darwin (1962) did not specify the basis for variation in worker behavior, the first requirement for the evolution of worker castes. It is possible that the allocation of workers to various tasks is also affected by the queen. For example, queens influence worker foraging activity, behaviorally in *Polistes* colonies (Reeve and Gamboa 1987) and via pheromones in colonies of honey bees (Free 1967; Jaycox 1970; Free et al. 1984), but there is presently no evidence of genetic variation among queens for these traits. Queen effects may cause workers to converge toward an average level of task performance. This would reduce the effects of worker genotypic variability, which lead to a divergence in worker behavioral phenotypes as seen here and elsewhere (Calderone and Page 1988; Frumhoff and Baker 1988; Robinson and Page 1988a). Observed behavioral variability within colonies may be influenced by both worker genotype and queen phenotype. Variability between colonies (reviewed by Rinderer and Collins 1986) may be affected by the genotypes of both workers and queens, if heritable variation exists for queen traits that influence worker behavior.

Genetic variation in worker behavior appears to have been necessary for the evolution of complex insect societies, but is the variation that exists today an adaptive feature of colony design? It has been proposed (Crozier and Consul 1976; Blum 1977; Crozier and Page 1985; Owen 1986) that intracolonial genetic variability may have selective value, if colonies with specialized worker genotypes function more effectively under a range of environmental conditions than colonies with a single, more generalized genotype. The results of a theoretical model (Page et al. 1988) suggest that

genetic variability for task performance may be advantageous and maintained in a population if worker specialization is a consequence of genotype, and leads to increased efficiency in task performance (Jeanne 1986).

In *Apis mellifera*, variability may be maintained at unusually high levels as a consequence of the disruption of natural population structure due to beekeeping practices. However, genetic variation in worker behavior does exist and may persist because colony-level selection is unable to eliminate it from populations, a consequence of behavioral dominance as discussed above. According to this view, polyandry is selected for by factors unrelated to the division of labor (Crozier and Page 1985; Sherman et al. 1988) and results in low heritabilities for traits due to non-additive effects of different phenotypes within colonies (Moritz and Southwick 1987; Page et al. 1988; Robinson and Page 1988b). Environmental heterogeneity may also prevent the emergence of a single optimal worker genotype (Hedrick 1986), thereby maintaining variability. Because queen honey bees apparently mate randomly, the existence of greater subfamily differentiation in some colonies than in others is expected, whether or not intracolonial genetic variation in worker behavior is adaptive.

Differences between subfamilies in task performance suggest that colony genetic structure constitutes a level of social organization in honey bees. Further insight into the role of colony genetic structure in the division of labor will be gained through studies of other social insect species, including those with monoandrous and polygynous societies.

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## References

Blum MS (1977) Ecological and social aspects of the individual behavior of social insects. Proc 8th Int Congr IUSSI, Wageningen, Holland, pp 54–59

Calderone NW, Page RE (1988) Genotypic variability in age polyethism and task specialization in the honey bee, *Apis mellifera* (Hymenoptera: Apidae). Behav Ecol Sociobiol 22:17–25

Contel EPB, Mestriner MA, Martins E (1977) Genetic control and developmental expression of malate dehydrogenase in *Apis mellifera*. Biochem Genet 15:859–876

Craig R (1980) Sex investment ratios in social hymenoptera. Am Nat 116:311–323

Crozier RH, Consul PC (1976) Conditions for genetic polymorphism in social hymenoptera under selection at the colony level. Theor Popul Biol 10:1–9

Crozier RH, Page RE (1985) On being the right size: male contributions and multiple mating in social Hymenoptera. Behav Ecol Sociobiol 18:105–115

Darwin CR (1962) The origin of species by means of natural selection or the preservation of favoured races in the struggle for life, 6th edn. Macmillan, New York

Del Lama MA, Soares AEE, Mestriner MA (1985) Linkage studies in *Apis mellifera* using biochemical and morphological markers. J Hered 76:427–430

Falconer DS (1981) An introduction to quantitative genetics. Ronald Press, New York

Free JB (1965) The allocation of duties among worker honeybees. Symp Zool Soc London 14:39–59

Free JB (1967) Factors determining the collection of pollen by honeybee foragers. Anim Behav 15:134–144

Free JB, Williams IH (1973) Genetic determination of honeybee (*Apis mellifera* L.) foraging preferences. Ann appl Biol 73:137–141

Free JB, Ferguson AW, Simpkins JR (1984) Influence of immature queen honeybees (*Apis mellifera* L.) on queen rearing and foraging. Physiol Entomol 9:387–394

Frumhoff PC, Baker J (1988) A genetic component to the division of labour within honey-bee colonies. Nature 333:358–361

Gary NE, Lorenzen K (1976) A method for collecting the honey-sac contents from honeybees. J Apic Res 15:73–79

Hedrick PW (1986) Genetic polymorphism in heterogeneous environments: a decade later. Ann Rev Ecol Syst 17:535–566

Hellmich RL, Kulincević JM, Rothenbuhler WC (1985) Selection for high and low pollen-hoarding honey bees. J Hered 76:155–158

Jaycox ER (1970) Honey bee queen pheromones and worker foraging behavior. Ann Entomol Soc Am 63:222–228

Jeanne RL (1986) The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp. Behav Ecol Sociobiol 19:333–341

Kaftanoglu O, Peng YS (1980) A washing technique for collection of honeybee semen. J Apic Res 19:205–211

Laidlaw HH (1974) Relationships of bees within a colony. Apiacta 9:49–52

Laidlaw HH (1977) Instrumental insemination of honey bee queens. Dadant & Sons, Hamilton

Laidlaw HH, Page RE (1984) Polyandry in honey bees (*Apis mellifera* L.): sperm utilization and intracolony genetic relationships. Genetics 108:985–997

Lindauer M (1952) Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. Z Vergl Physiol 34:299–345

Lindauer M (1955a) The water economy and temperature regulation of the honeybee colony. Bee World 35:62–72, 81–92, 105–111

Lindauer M (1955b) Schwarmbienen auf Wohnungssuche. Z Vergl Physiol 38:521–557

Moore AJ, Breed MD, Moore MJ (1987) The guard honey bee: ontogeny and behavioural variability of workers performing a specialized task. Anim Behav 35:1159–1167

Moritz RFA (1983) Homogeneous mixing of honeybee semen by centrifugation. J Apic Res 24:249–255

Moritz RFA, Southwick EE (1987) Phenotype interactions in group behavior of honey bee workers (*Apis mellifera* L.). Behav Ecol Sociobiol 21:53–57

Morse RA (1961) Swarm orientation in honeybees. Science 141:357–358

Nowogrodzki R (1983) Individual differences and division of labor in honey bees. PhD Dissertation, Cornell University
Nowogrodzki R (1984) Division of labour in the honeybee colony: a review. Bee World 65:109–116
Nunamaker RA, Wilson WT (1980) Some isozymes of the honey bee (*Apis mellifera* L.). Isozyme Bull 13:111–112
Oettingen-Spielberg T (1949) Ueber das Wesen der Suchbiene. Z Vergl Physiol 15:431–487
Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton
Owen RE (1986) Colony-level selection in the social insects: single locus additive and nonadditive models. Theor Popul Biol 29:198–234
Page RE (1986) Sperm utilization in social insects. Ann Rev Entomol 31:297–320
Page RE, Metcalf RA (1982) Multiple mating, sperm utilization, and social evolution. Am Nat 119:263–281
Page RE, Robinson GE, Calderone NW, Rothenbuhler WC (1988) Genetic structure, division of labor, and the evolution of insect societies. In: Breed MD, Page RE (eds) The genetics of social evolution. Westview Press, Boulder
Reeve HK, Gamboa GJ (1987) Queen regulation of worker foraging in paper wasps: a social feedback control system (*Polistes fuscatus*, Hymenoptera: Vespidae). Behaviour 102:147–167
Rinderer TE, Collins AM (1986) Behavioral genetics. In: Rinderer TE (ed) Bee genetics and breeding. Academic Press, New York
Robinson GE, Page RE (1988a) Genetic determination of guarding and undertaking in honey-bee colonies. Nature 333:356–358
Robinson GE, Page RE (1988b) Genetic basis for division of labor in an insect society. In: Breed MD, Page RE (eds) The genetics of social evolution. Westview Press, Boulder
Seeley TD (1983) Division of labor between scouts and recruits in honeybee foraging. Behav Ecol Sociobiol 12:253–259
Seeley TD (1985) Honeybee ecology: A study of adaptation in social life. Princeton University Press, Princeton
Seeley TD, Morse RA, Visscher PK (1979) The natural history of the flight of honeybee swarms. Psyche 86:103–113
Sekiguchi K, Sakagami SF (1966) Structure of foraging population and related problems in the honeybee, with considerations on the division of labour in bee colonies. Hokk Nat Agric Exp Stn Rep 69:1–65
Sherman PW, Seeley TD, Reeve HK (1988) Parasites, pathogens and polyandry in social Hymenoptera. Am Nat 131:602–610
Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, San Francisco
Visscher PK (1983) The honey bee way of death: necrophoric behaviour in *Apis mellifera*. Anim Behav 31:1070–1076
Wilson EO (1985) The sociogenesis of insect colonies. Science 228:1489–1495
Wilson EO (1987) Causes of ecological success: the case of the ants. J Anim Ecol 56:1–9
Winston ML (1987) The biology of the honey bee. Harvard University Press, Cambridge