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REVIEW ARTICLE

Honeybee colony drone production and maintenance in accordance with environmental factors: an interplay of queen and worker decisions

K. E. Boes

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Abstract Social insect colonies display a remarkable ability to adjust investment in reproduction (i.e., production of sexuals) in accordance with environmental conditions such as season and food availability. How this feat is accomplished by the colony's queen(s) and workers remains a puzzle. Here, I review what we have learned about this subject in the European honeybee (*Apis mellifera*), specifically with regard to a colony's production of males (drones). I identify five environmental conditions that influence colony-level patterns of drone production and then define five stages of drone rearing that are accomplished by the queen and workers. Using this framework, I detail our current understanding of how the queen or workers adjust their actions at each stage of drone rearing in response to each of the environmental conditions. Future investigations of this topic in honeybees and other social insect societies will lead to a better understanding of how colonies manage to flexibly and efficiently allocate their resources under changing environmental conditions.

Keywords Honeybees · Drones · Colony organization · Sex allocation · Cooperation

Introduction

Since Darwin (1874), biologists have sought to understand the ways in which natural selection shapes the ability of organisms to adjust their investment in the sexes. An organism's allocation of resources to male versus female reproductive function is termed its sex allocation (Charnov, 1982). Like organisms, social insect colonies face the challenge of appropriately allocating resources to life history traits such as reproduction, in general, and between male and female reproductive function, in particular.

Honeybee colonies reproduce in two distinct ways: by swarming, a fission process in which the queen and over half of the worker bees leave to establish a new colony (a "female" mode of reproduction), and by producing and maintaining males (hereafter drones), whose sole apparent function is to mate with virgin queens in the population. This latter "male" mode of reproduction allows a colony to introduce the genes shared by its members into other colonies in the population and is the focus of this paper.

Honeybee colonies actively regulate their investment in male reproductive function. In colonies of *Apis mellifera*, drones typically compose 5–10% of the adult population (Page and Metcalf, 1984; Seeley and Morse, 1976). However, a colony is able to adjust its investment in drones in accordance with environmental factors (Page and Metcalf, 1984). This colony-level adjustment must arise from the action and interactions of the queens and workers, but how it actually occurs presents an open and interesting question in social insect biology (Bourke and Franks, 1995). The purpose of this paper is to organize and review what we know (and what we have yet to learn) about drone production in colonies of the European honeybee, *Apis mellifera*.

The organization of this paper is as follows. I begin by identifying five environmental conditions and explaining how each affects colony-level patterns of drone rearing ("Colony-level patterns of drone production based on environmental factors"). Next, I define the key stages involved in drone production and maintenance and focus

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K. E. Boes (✉)
Department of Zoology, Michigan State University,
203 Natural Sciences Bldg., East Lansing, MI 48824, USA
e-mail: wharton2@msu.edu

on how drone rearing at each stage changes in relation to the five environmental conditions ("Key stages in drone production and maintenance"). I conclude by emphasizing the importance of studies that examine how social insect colony sex allocation is shaped by the actions and interactions of the queen(s) and workers.

Colony-level patterns of drone production based on environmental factors

Honeybee colonies regulate their production and maintenance of drones in accordance with several environmental factors. In this section, I identify five of these factors and discuss colony patterns of drone rearing in relation to each.

Season

The number of drones present in a honeybee colony varies over the course of a year. A colony's drone population increases during the spring and reaches a peak in the late spring or early summer. Although this peak in drone production also coincides with the peak in worker production, it is during this time of year that colonies produce the highest proportion of drone brood (Free and Williams, 1975). This peak occurs just prior to the population's main swarming season, when virgin queens are most abundant (Allen, 1958; Allen, 1965b; Lee and Winston, 1987; Page, 1981). As a result, colonies have the greatest number of drones during the time of year when drones are most likely to successfully mate. The colony's drone population slowly decreases throughout the late summer and into the fall, and typically dwindles to zero by winter.

The seasonal factors that influence these trends in drone production are unknown. While colonies might adjust drone production in relation to season itself (length of day and temperature), the trends more likely arise from a combination of season and other environmental cues (size of colony and availability of food) that vary with season. Similarly, colony microclimate cues, such as the concentration of carbon dioxide, likely play an important role (Buhler et al. 1983).

Size of colony

Honeybee colonies refrain from producing drones until the colony has a sufficiently large population of adult workers. The population of adult workers in a colony is naturally low following a swarming event, and swarms that establish new colonies prevent early drone production by not constructing drone comb (the wax cells in which drones are reared) until an average of 22 days after establishment (Lee and Winston, 1985). Once established, larger swarms build a greater proportion of drone cells more quickly than do smaller swarms, indicating a strong effect of swarm size on drone comb investment (Henderson, 1991). In addition, small swarms that are composed of fewer than 10,000 workers sometimes build little or no drone comb at all, indicating that small colonies limit their investment in drones until they grow larger (Lee and Winston, 1985).

As small colonies increase their production of brood, they also increase the proportion of drone brood (Free and Williams, 1975). However, once colonies reach a large size (more than 12,000 adult workers), there does not appear to be any relationship between the number of workers reared and the percentage of drone brood in the colony (Page and Metcalf, 1984). Colonies therefore reach an upper limit in their investment in drones.

Food availability

Drones are more costly to produce and maintain than workers (Hrassnigg and Crailsheim, 2005; Seeley, 2002), so colonies should regulate drone production in accordance with the availability of food. Seeley and Mikheyev (2003) confirmed this in a controlled experiment. They maintained a group of colonies in a food-plentiful environment and observed that the colonies produced similar amounts of drone brood. They then transferred the colonies to an island with very few food sources and experimentally manipulated food availability by provisioning half of the colonies with sugar water and leaving the other colonies to rely on only the island's limited food sources. On the island, the food-supplemented colonies continued to produce many drones, but the non-supplemented colonies lowered their production of drones.

Honeybee colonies also decrease their production of workers when foraging conditions are poor (Schmickl and Crailsheim, 2001, Schmickl and Crailsheim, 2002), but it is unknown how honeybee colonies jointly regulate drone and worker production during periods of low food availability. Since the value of drones likely changes in relation to workers throughout the year (see "Season"), colonies might be expected to display seasonal trends in how they jointly produce drones and workers in response to food availability, but this has not yet been tested.

Amount of drone brood and number of drones already present in the colony

Colonies adjust their production of immature drones (eggs, larvae, and pupae; hereafter drone brood) in accordance with the amount of drone brood already present. Specifically, when drone brood is added to colonies, the colonies lower their production of additional drones (Free and Williams, 1975). This demonstrates that the presence of drone brood in a colony inhibits the colony's production of additional drones. Drone production is therefore regulated by a negative feedback process.

Studies that tested whether colonies adjust their production of drones in accordance with the number of adult drones present have produced mixed results. Rinderer et al. (1985) added adult drones to colonies and found that the colonies subsequently lowered their drone production. However, Henderson (1994) removed drones from colonies and found that colonies did not increase drone production. These mixed results call into question whether, and if so how, honeybee colonies can assess the size of their population of adult drones.

Future work might better examine the trade-offs that colonies face by investing in drones. Drone rearing does not appear to trade off with worker rearing, because colonies that are prevented from investing in drones do not produce more workers than colonies allowed to rear drones (Allen, 1963; Allen, 1965a; Page and Metcalf, 1984). Drone rearing might trade off with honey yield, an important means by which colonies survive the winter, but there is both supporting and contradictory evidence that drone rearing affects honey yield (Allen, 1965a; Johansson and Johansson, 1971; Seeley, 2002). These results raise questions about the life history trade-offs that honeybee colonies face when investing in drones.

Queen presence/absence

The environmental factors discussed above have only been evaluated in colonies where the queen is present, termed queenright colonies. In queenright colonies, the queen produces approximately 99.9% of the colony's adult males (Visscher, 1989). If the queen becomes inviable or dies, the colony will attempt to rear a replacement queen. If that attempt fails and the colony becomes "hopelessly" queenless, drones become the sole source through which the colony can pass along genes. Accordingly, the colony increases its investment in drones relative to workers. This happens naturally because some workers reared in queenless colonies develop functional ovaries and are able to lay drone (unfertilized) but not female (fertilized) eggs (though an exception is the Cape honeybee, *Apis mellifera capensis*, in which workers are capable of laying female eggs) (Martin et al., 2002).

Workers begin laying eggs after losing the queen, though there is substantial variation in when this occurs across various subspecies. In queenless colonies of *Apis mellifera ligustica*, workers begin laying eggs around 24 days after the queen's disappearance, and their production of drone eggs is short and synchronous (Page and Erickson, 1988). Identification of the workers that are most successful in laying eggs is difficult, because workers consume or "police" many of the eggs (Miller and Ratnieks, 2001). Additionally, subfamilies of workers vary in their tendencies to produce and consume eggs (Martin et al., 2004; Robinson et al., 1990), and younger workers appear to be more successful at laying eggs than older workers (Delaplane and Harbo, 1987). Despite the oophagy that occurs, worker egg-laying can result in 6,000 additional adult drones for a queenless colony (Page and Erickson, 1988). However, because the workers cannot produce new workers or a new queen, the colony cannot maintain these drones for long before the colony dies.

Key stages in drone production and maintenance

Colonies produce and maintain drones in a multi-staged sequential process (Fig. 1). At each stage, either the workers or the queen have the opportunity to shape the colony's investment in drones. In this section, I examine each of these stages in detail. For each stage, I present a brief overview of the stage's importance for colony drone production, review how the bees modify the colony's investment in drones in response to the environmental factors listed in the section "Colony-level patterns of drone production based on environmental factors", and highlight aspects of the stage that are not well understood. A summary of this section is provided in Table 1.

Workers build comb

Workers build the wax cells that are used by the colony to store food and rear bees. These cells are either small in size (worker cells) or larger in size (drone cells). This cell size dimorphism likely arose or was maintained through selection on drones for large body size, as small worker-sized drones experience a lower reproductive success (Berg et al., 1997). Drone cells typically constitute 15–20% of the total comb area (Seeley and Morse, 1976). Though bees occasionally reshape one type of cell into the other type under unnatural conditions (see Free and Williams, 1975), they typically do not alter the wax comb that has already been built. Since drones are not normally reared in the smaller worker cells, the number of drone cells in a colony limits the number of drones that can be reared at any one time. However, if colonies are provisioned with an excessive amount of drone comb, they do not use all of it for rearing drones, indicating that a colony's regulation of drones is determined by more factors than just the amount of comb in the colony (Allen, 1965a). Of all the stages involved in drone production, the construction of comb has been the most extensively studied. For an extensive review of the factors that govern comb construction in honeybees, see Pratt (2004).

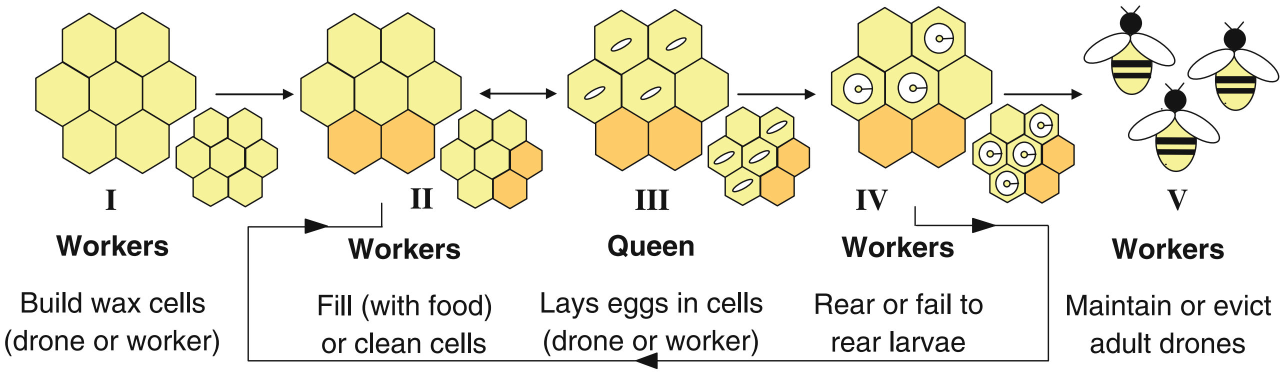

Fig. 1 (Reproduced with permission from Wharton et al., 2007.) Drone production and maintenance in a honeybee colony: a sequence of actions taken by the workers and the queen. At each step, the bees have an opportunity to alter the colony's investment in drones in response to environmental conditions. *Arrows* indicate typical sequences of events. Drone cells are larger than worker cells, and drones are reared in these larger cells (*I*). The worker and drone cells are used either for food storage (nectar and pollen; *darker cells* in diagram) or are cleaned in preparation for rearing brood (*II*). The queen typically lays unfertilized (drone) eggs into drone cells and fertilized (female) eggs into worker cells (*III*). Workers then tend the larvae, but do not necessarily raise all of the larvae to adulthood (*IV*). Adult drones remain colony members until they mate with a virgin queen in the population, die or are evicted by workers (*V*). See "Workers build comb, Workers clean cells or fill cells with nectar, Queens lay eggs, Workers rear/fail to rear larvae, Workers maintain or evict drones" of this paper for details of each stage

Workers build drone comb mostly in the spring and early summer, indicating that season influences drone comb construction (Free, 1967). Two lines of evidence support this assertion. First, swarms established earlier in the year produce more drone cells than swarms (of an identical size) established later in the year (Lee and Winston, 1985). Second, colonies build the highest proportion of drone cells in May through July (Free and Williams, 1975). This occurs despite the fact that the authors in that study controlled for both food availability and drone brood presence by supplementing their colonies with sugar syrup throughout the year, and by removing built drone comb on a weekly basis. These results therefore are consistent with the idea that the season itself (day length and temperature) influences drone comb construction. Colony size also affects drone comb construction; see "Size of colony" for details.

Drone comb construction is regulated by negative feedback. Workers reduce their construction of drone comb when it is already present (Free, 1967; Free and Williams, 1975; Pratt, 1998), and they further reduce drone comb construction if drone brood is present as well (Pratt, 1998). Based on these trends, one might expect that workers reduce drone comb construction when the colony contains an abundance of adult drones, but this remains an open question.

Drone comb construction is influenced by whether or not the colony has a queen. When the colony is queenless but workers are rearing queens, the workers build a higher proportion of drone cells (Free, 1967), but less comb overall, than do queenright colonies (Pratt, 2004). In queenright colonies, food must be available for workers to construct any comb at all (Pratt, 2004), but how the amount of food available influences the colony's relative investment in drone cells to worker cells is largely unknown. One study suggested that colonies did not alter drone comb construction depending on food availability, but that study used too few colonies to make a statistical inference (Sasaki and Obara, 2001).

Workers clean cells or fill cells with nectar

Worker bees perform the actions of cleaning the brood cells and storing or removing food from the cells. When the cells have been cleaned of debris and do not contain any pollen or nectar, they are available to receive an egg from the queen (Winston, 1987). Since the queen lays eggs continuously and workers clean and use cells constantly, whether a particular cell is used for food storage or for rearing brood depends on a dynamic interplay of actions taken by both the queen and the workers.

The use of drone and worker cells for egg deposition appears to be independent of certain worker decisions. In one study, the decision of the queen to deposit an egg in a drone or worker cell was not constrained by the decisions of workers to fill drone and worker cells with nectar (Wharton et al., 2007). In another study, workers were equally likely to clean either worker or drone cells (Sasaki et al., 1996), allowing both types to be available for egg deposition. Although the decisions of the queen and workers might be independent in some circumstances, they are likely dependent when a colony has limited cells available for brood or food. Future work might address whether in such cases the workers primarily limit the cells

Table 1 Current understanding of how colonies adjust drone production in relation to environmental conditions (rows) for each of the stages involved in drone production (columns)

	Workers build comb	Workers clean cells/fill cells with nectar	Queen lays eggs	Workers rear/fail to rear larvae	Workers maintain/evict adult drones
Season	D comb construction is highest in the spring and early summer	D cells are used primarily for brood rearing in spring/summer and primarily for nectar in fall	D egg production is higher in spring–early summer than in late summer–fall	Survival of D larvae is variable across season; survival is lowest in the fall	D eviction is higher in the fall than in spring or summer
Size	Larger colonies build more D comb, and build it more quickly, than smaller colonies	Unknown	Unknown	Unknown	Unknown
Food availability	Colonies must have nectar intake to build any comb at all; unknown how food affects the proportion of D comb built	Unknown	Egg production is lower during poor food conditions; unknown how this affects relative production of D and W eggs	Fewer brood survive under poor foraging conditions; relative survivals of D and W brood are unknown	D eviction is higher in unfed colonies than in fed colonies
Amount of drone brood and adult drones present in colony	D comb alone inhibits D comb construction; D brood enhances this inhibition. Unknown whether adult D inhibits D comb construction	Unknown	D brood inhibits D egg production; unknown whether adult D inhibits D egg production	Survival of D larvae is lower when colonies contain D brood; unknown whether adult D influences survival of D larvae	Unknown
Queen presence/absence	Queenless colonies build less comb overall, but a greater proportion of the comb built is D comb	Unknown	If queen is absent, workers lay D but not W eggs (some exceptions; see text)	Survival of queen-laid D brood increases in queenless colonies; low survival of worker-laid D brood	D eviction higher in queenright colonies than in queenless colonies

See "Workers build comb, Workers clean cells or fill cells with nectar, Queens lay eggs, Workers rear/fail to rear larvae, Workers maintain or evict drones" of this study for additional details

D drone, *W* worker

available to receive eggs, or whether the queen has any ability to limit the cells available for food storage.

Whether workers respond to environmental factors for cell cleaning activities or for storing food remains largely an open question. For instance, drone comb contains mostly brood in the early summer and mostly food in the early fall (Free and Williams, 1975); how does this occur? This seasonal pattern might arise because workers refrain from filling drone cells with food until later in the season, because queens reduce the number of eggs they lay into drone cells later in the season, or because of some combination of these two factors. To date, few studies have examined how the use of a cell depends on colony size, food availability, the presence of drones or the colony's queen status. This paucity of research likely stems from the difficulty of determining how patterns of brood and food deposition arise from a complex interplay between actions taken by the workers and the queen (Camazine, 1991).

Queen lays eggs

The queen honeybee contributes to colony brood production by laying drone (unfertilized) eggs into available drone cells and laying worker (fertilized) eggs into available worker cells. She determines the cell size by briefly inspecting and measuring the diameter of each cell she visits with her legs (Koeniger, 1970). She is usually extremely precise in laying the correct type of egg in the correct type of cell (Ratnieks and Keller, 1998), though for reasons yet unknown there are situations in which she makes "mistakes" (see Berg et al., 1997; Haydak, 1958; Wharton et al., 2007).

The queen likely has an ability to shape brood production patterns by choosing whether to lay eggs in either drone or worker comb. Consistent with this idea, the queen sometimes lays drone and worker eggs in a ratio that deviates from the ratio of available drone and worker cells (Henderson, 1991; Wharton et al., 2007). The eggs eventually develop into larvae, which can potentially be consumed by the workers (see "Workers rear/fail to rear larvae"). Therefore, to determine whether the queen adjusts her drone egg production in response to environmental conditions, it is necessary to examine the colony's egg (rather than larvae or pupae) sex allocation. Only a few studies to date have examined queen egg-laying decisions, and I outline those results here.

Sasaki and Obara (2001) examined the interaction of season and food availability on the queen's egg-laying decisions. They found that when colonies are continuously supplied with food throughout the year, queens lay more drone eggs in the spring and summer than in the fall. Additionally, while the queen lays few drone eggs in the fall independent of food condition, in the late spring she appears to produce a higher proportion of male eggs during good food conditions than during poor food conditions. However, that study used a within-subjects design and did not control for the order of food condition treatments. Therefore, how the queen alters her production of drone eggs in response to food availability should be tested in future studies. Additionally, future studies might examine whether the queen's production of drone eggs changes in response to colony size.

The honeybee queen's production of drone eggs is regulated by negative feedback. Studies supporting this found that queens who had recently laid drone eggs subsequently produced fewer drone eggs than queens who had recently laid only worker eggs (Sasaki et al., 1996; Wharton et al., 2007). In the study by Wharton et al. (2007), the authors followed the eggs to the pupal stage and found that the queen's egg-laying decisions influenced colony-level drone production patterns. Additionally, the authors controlled for season, colony size and food availability, and found that the decisions of the queens were not constrained by worker decisions to fill cells with nectar. That study therefore demonstrated that the queen altered her egg-laying patterns by detecting and responding to either her own previous egg-laying experience or the presence of drone brood in the colony. Which of these two factors was a greater determinant of queen egg-laying patterns is an attractive topic for future study.

Workers rear/fail to rear larvae

Workers sometimes consume a portion of their colony's developing larvae (Woyke, 1977). Workers presumably eliminate larvae when environmental conditions are unfavorable for rearing brood. These actions might serve to recycle colony resources before the larvae become too expensive for the colony to support (Webster et al., 1987). Consistent with this idea, workers selectively destroy younger larvae, which would cost more to rear to maturity than older larvae (Schmickl et al., 2003; Schmickl and Crailsheim, 2001, Schmickl and Crailsheim, 2002; Woyke, 1977). Additionally, although workers rarely consume pupae, they preferentially consume younger rather than older pupae (Newton and Michl, 1974).

The tendency of workers to eliminate males fluctuates over the season and with the colony's queen status. During the spring and fall, workers consume more drone brood than worker brood, but in the summer the survivals of drone and worker brood are high and approximately equal (Fukuda and Ohtani, 1977; Woyke, 1977). These results suggest that workers consume more drone larvae in the fall when drones are of little value to the colony. In queenless colonies, the survival of queen-laid drone and worker larvae increases (Woyke, 1977), although once workers begin to lay eggs, many worker-laid drone eggs are destroyed (Miller and Ratnieks, 2001).

The tendency of workers to eliminate males is influenced by the amount of drone brood in the colony. This was confirmed in a recent study by Wharton et al. (2008). They manipulated the abundance of older male brood in colonies and found that the survival of younger male larvae was lower when the abundance was increased than when it was decreased. Meanwhile, the survival of worker larvae was high across colony conditions. These results suggest that the brood rearing decisions of workers assist the colony in regulating its investment in male reproductive function.

The tendency of workers to eliminate males likely is influenced by colony food conditions, but how food conditions affect the relative rates of cannibalism for drone and worker larvae awaits future study. The tendency of workers to consume worker larvae increases during periods of poor food availability (Schmickl and Crailsheim, 2001). Interestingly, under poor colony food conditions, the workers preferentially consumed younger (less than 3 days old) rather than older (4–5 days) larvae and also preferentially withheld nursing from the younger larvae (Schmickl et al., 2003; Schmickl and Crailsheim, 2001, Schmickl and Crailsheim, 2002). The colonies in these studies contained only worker brood, so it is unknown how the workers would have treated drone larvae under similar conditions.

In general, the circumstances under which workers cannibalize larvae are poorly understood. This is largely because very few studies to date compare the survival of drone and worker larvae in a manipulative experiment. An exception to this is the study mentioned above by Wharton et al. (2008). I suggest that we need more manipulative studies to determine whether and under what conditions workers selectively destroy drone or worker larvae. To selectively destroy either drone or worker larvae, workers would need to distinguish between the two. While it is unknown if workers can distinguish between young drone and worker larvae based on cell size alone, workers are likely able to distinguish between the two sexes based on chemical cues once the larvae are 3–4 days old, which is approximately 7 days after the queen lays eggs (Sasaki et al., 2004; see also Haydak, 1958). Much more work remains to be done in this area.

Workers maintain or evict drones

Besides producing drones, colonies maintain adult drones. Adult drones are costly for the colony to maintain because a drone consumes approximately four times the amount of food that a worker consumes (Winston, 1987). Colonies will maintain a drone until one of the following happens: the drone mates successfully with a virgin queen (drones die upon mating), the drone dies or workers evict the drone from the colony in a process known as “drone eviction.”

During drone eviction, workers force drones out of the colony and prevent them from reentering (Free, 1957). Since the evicted drones cannot access the colony’s food stores, they soon die of starvation. A drone’s age appears to affect his likelihood of being evicted; Free (1957) observed that workers selectively harassed older drones while permitting younger drones to remain. Drone eviction takes place gradually over the autumn and is most likely to occur on warmer days when the workers are more active in the colony (Morse et al., 1967). Although the exact cues that trigger drone eviction are unknown, it is thought that workers evict drones when the expected cost of maintaining drones outweighs the expected fitness benefit.

Since the fitness benefit of keeping and maintaining drones fluctuates with environmental conditions, colonies exhibit greater levels of drone eviction under particular environmental circumstances. Workers evict more drones in the fall than in the spring (Morse et al., 1967); drone eviction before the fall rarely occurs. During the fall, queenright colonies evict more drones during periods of poor food availability (Free and Williams, 1975). Additionally, when foraging conditions are poor in the fall, queenright colonies evict more drones than do queenless colonies; when foraging conditions are good, the colony’s queen status does not affect the amount of drone eviction (Free and Williams, 1975).

There is still much to learn about drone eviction. In particular, it is unknown how colony size (or a reduction in colony size following a swarm event) affects drone eviction. Observations support the idea that colony size might play a role: when frames of brood and bees were brought into a small (2-frame) observation hive during midsummer, workers soon evicted the drones (Boes, personal observation), although this does not always happen (Free, 1957). Additionally, future research should better elucidate the proximate cues that trigger the workers to recognize that their colony has an excess number of drones.

Conclusions

Drones are an important, but costly, investment for the honeybee colony, and so colonies regulate the number of drones they produce. This regulation of drone production arises from the actions and interactions of the queen and workers, who must respond to environmental factors that affect the expected fitness value of rearing drones. To date, research with honeybees has elucidated the responses of colony members to several environmental influences. However, this work is by no means exhaustive, and has only begun to shape our understanding of honeybee brood production dynamics and colony organization. Future work in this area is crucial to better understand how the individuals in social insect colonies coordinate their actions to achieve adaptive colony decisions.

The emerging picture of brood production in honeybees is that the queen and workers share control over their colony's sex allocation. Historically, the queen was viewed as an egg-laying "machine" that did not regulate colony-level patterns of sex allocation. Recent evidence suggests that this previous view is incorrect; the queen's egg-laying decisions can shape her colony's regulation of investment in male reproductive function (see "Queen lays eggs"). Additionally, workers play an important role in colony sex allocation patterns by building and preparing wax cells to hold the brood, rearing or destroying the larvae and maintaining or evicting adult drones (see "Workers build comb, Workers clean cells or fill cells with nectar, Workers rear/fail to rear larvae, Workers maintain or evict drones"). Together, the decisions of the queen and workers provide a colony with many stages and strategies by which it might adjust sex allocation in response to environmental conditions.

In many social insect species, the queen and workers are expected to favor different sex allocation optima (Hamilton, 1964; Strassmann, 2001; Trivers and Hare, 1976). This queen–worker conflict over sex allocation arises because of the haplodiploid system of sex determination, by which workers are typically three times more related to their sisters than to their brothers, whereas the queen is equally related to her daughters and sons. The notion of conflict within social insect colonies has inspired a tremendous research effort involving both empirical work and theory, which has led to many advances in our knowledge of colony dynamics and resource allocation (Crozier and Pamilo, 1996). In species characterized by queen–worker conflict, the extent to which colony members can influence sex allocation can provide insights into the distribution of power within the colony, where power is defined as the ability to do or act in situations of conflict (Beekman et al., 2003; Beekman and Ratnieks, 2003).

In species in which the queen mates with many males (as in the honeybee), queen–worker conflict over sex allocation is theoretically very small or absent (Moritz, 1985; Ratnieks et al., 2006). Species that exhibit an extremely high queen mating frequency include the honeybees (Palmer and Oldroyd, 2000), the Florida harvester ant *Pogonomyrmex badius* (Rheindt et al., 2004), and the African army ant *Dorylus anomma* (Kronauer et al., 2004). In these species, queens and workers theoretically "agree" on their colony's sex allocation. In species characterized by an absence of queen–worker conflict, the extent to which colony members can influence sex allocation can provide important insights into how colonies might efficiently and flexibly respond to environmental conditions.

Whether or not there is conflict between the queen and workers over colony sex allocation, the study of queen and worker influence on colony sex allocation patterns has great potential to advance our understanding of the dynamics and organization of social insect colonies. Increasingly, researchers are recognizing social insects as an excellent model system for addressing questions on how living systems organize their individual components to cope with a dynamic environment (Camazine et al., 2001). Research that elucidates the effects of queen and worker decisions on colony sex allocation will therefore broaden our understanding of how social insect colonies, and in turn other complex living systems, coordinate their group members to cope with environmental uncertainty. This research is also likely to provide key insights into the behavioral ecology of social insects and, more broadly, the evolution of cooperation.

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