Insectes Soc. 50 (2003) 134 – 138
0020-1812/03/020134-05
DOI 10.1007/s00040-003-0638-8

Insectes Sociaux

Research article

Reproductive decisions by honey bee colonies: tuning investment in male production in relation to success in energy acquisition

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Received 6 May 2002; revised 21 October 2002; accepted 17 December 2002.

Summary. One way to understand the adaptive design of the life history of a social insect colony is to view the colony as having an investment policy whereby it allocates limited resources among the various physiological functions fostering its growth, survival, and reproduction. Prior work has shown that energy is a limited resource for a honey bee colony and that a colony faces a strong trade-off between energy investment in current reproduction and future survival. Given these facts, we hypothesized that a colony might have a flexible energy investment policy, whereby it adjusts its investment in reproduction in relation to its success in acquiring energy. To test this hypothesis, we manipulated the energy acquisition of colonies and looked for an effect on their reproductive efforts. We found that when a colony experiences difficulty building the energy reserve it needs to survive to the next reproductive season, it trims its allocation of energy to drone production and possibly also to drone maintenance. The mechanisms of social physiology which enable a colony to adjust its investment in male reproductives in relation to its energy budget remain a mystery.

Key words: Apis mellifera, cost of reproduction, honey bees, life history evolution, reproductive decision, trade-offs.

Introduction

Whenever two or more processes within an individual compete for limited resources, the individual is faced with a physiological trade-off problem (reviewed in Stearns, 1992; Roff, 2001). The solution to this problem is a partitioning of the limited resources in such a way that optimally balances investment in current reproduction and future survival, thereby maximizing the individual's lifetime reproductive output (Cody, 1966; Williams, 1966, p. 172; Schoener, 1971; Roff, 1992). Numerous studies of individual organisms have found that they experience physiological trade-offs, for example in female red deer where a decision is made to allocate limited resources between milk vs. fat reserves (Clutton-Brock et al., 1982), in beech trees where a decision is made to allocate materials and energy between seeds vs. wood and leaves (Rohmeder, 1967), in fish where a decision is made to allocate "surplus" energy between gametes vs. body tissue (Ware, 1982), and in lace bugs and bean beetles where decisions are made to allocate resources between egg production and later survival (Tallamy and Denno, 1982; Tatar et al., 1993). To date, however, few studies have been made with colonies of social insects to see if they too experience physiological trade-offs, even though this is a subject essential to understanding the development patterns and life histories of these colonies.

A recent experimental study with honey bee colonies, in which investment in males was manipulated by providing or withholding drone comb, found a large trade-off between a colony's production of male reproductives (drones) and its accumulation of energy reserves (honey stores) (Seeley, 2002). Over the summer season, colonies that invested little in rearing drones built up energy reserves nearly double those of colonies that invested normally in rearing drones: 48.8 vs. 25.2 kg of honey, respectively. This finding confirms the longheld belief of beekeepers that it is worthwhile to take measures to inhibit a colony's drone rearing in order to increase its honey yield (see, for example, Langstroth, 1866, p. 51). Evidently, energy is a limited resource within a honey bee colony. Given that a honey bee colony experiences a trade-off between current reproduction and energy reserve, and given that the size of a colony's energy reserve strongly influences its survival to the next reproductive season (Seeley and Visscher, 1985), it is clear that a honey bee colony also experiences a trade-off between current reproduction and future survival. In considering this trade-off between energy investment in reproduction and survival, we wondered if a colony might possess mechanisms of social physiology that enable it to tune its investment in current reproduction in relation to its success in acquiring energy. For instance, a colony might trim its allocation of energy to drone production and maintenance if it is experiencing difficulty building the energy reserve it needs to survive winter. To test this hypothesis, we conducted an experimental study in which we manipulated the energy acquisition of honey bee colonies and looked for an effect on their reproductive efforts.

Methods

The general plan of the study was to move 10 colonies of honey bees to a location with little natural forage, give half the colonies a daily ration of concentrated sugar solution, and compare the fed and unfed colonies in terms of drone production and maintenance.

On April 28, 2000, 14 nucleus colonies were established in Ithaca, New York (42°26′N, 76°30′W). Each colony was installed in a 10-frame Langstroth hive with full-depth frames. Each colony consisted initially of a young Buckfast queen (newly purchased from R. Weaver Apiaries, Navasota, Texas); 2 frames filled with brood, pollen, and honey and covered with worker bees; 1 empty frame covered with bees; and 2 frames filled with honey but without bees. All the frames were chosen carefully so that none contained patches of drone cells. (By limiting the drone cells in each colony's hive to those in the frames of drone comb (see below), we simplified the measurement of the drone brood in each hive.) On May 8, each colony was given the 5 additional frames it needed to fill its hive: 3 more frames of empty worker comb and 2 frames of empty drone comb. In a natural nest of honey bees, 17–19% of the comb area is devoted to drone comb (Weiss, 1962; Seeley and Morse, 1976), so by giving the colonies 2 out of 10 frames of drone comb we gave them a normal supply of the cells needed to rear drones. The 2 frames of drone comb were positioned in the #3 and #8 positions in the hive, hence the drone comb was placed in its natural location, on the edge of the broodnest (Taber and Owens, 1970). By the end of May the colonies had grown to cover most of the frames in their hives and had begun to rear drones. On June 3, each colony was given a second, full-depth hive body containing 8 empty frames of worker comb and 2 empty frames of drone comb, arranged as described above. Also, to assess the development of each colony, we measured the number of frames of worker brood in each hive. To do so, we judged by eye whether each frame was 1/4, 1/2, 3/4, or entirely filled with brood.

On June 7, we began a series of weekly measurements of the amount of drone brood in each colony. The procedure for measuring a colony's drone brood was as follows: remove a frame of drone comb, place a grid with squares 1 cm^2 over one side of the comb, count the number of squares lying over cells containing drone brood, and then repeat the procedure for the other side of the comb. This procedure was repeated for each frame of drone comb in each colony's hive. The grid was a combless hive frame with strands of fine, light-green string (dental floss) strung tightly across it at 1 cm intervals. Looking through this grid at a frame of drone cells, we could see easily larvae and even eggs. These measurements were taken 6 times, on June 7, 14, 21, and 28, and on July 5 and 12.

On June 14, we began a series of measurements of the weight of each colony's hive. Each hive's weight was measured after sundown, when all the bees were inside, by lifting it onto platform scales with 0.1 kg precision. The weight recorded represented the total weight of the hive proper, the adult bees and brood, and the food stores. These hive weight measurements were performed 4 times, on June 14 and 26, and July 5 and 12.

On the morning of June 15, the 10 strongest colonies were moved 240 km north to the Cranberry Lake Biological Station (44°09′ N, 74°48′ W) in the Adirondack State Park, Saint Lawrence County, in northern New York State. Unlike in Ithaca, where the landscape consists of fields, tracts of woods, and residential areas, and bee forage is plentiful, at the CLBS the landscape consists of vast expanses of woods, lakes, and bogs, and bee forage is sparse. By moving the colonies to this setting with poor forage, we gained control of the energy intake of our colonies (see below). The colonies were placed in pairs, two per hive stand, in one apiary surrounded by electric fence for protection from black bears (*Ursus americanus*). Once at the CLBS, each colony was equipped with a dead bee trap (Gary, 1960) and daily counts were begun of the number of dead adult and pupal drones appearing in each colony's trap. The effectiveness of the traps had been tested in Ithaca by putting into each hive 50 dead and labeled drones in the afternoon and seeing how many were in the traps the next morning. On average, 96% of the drones were recovered. The dead bee traps were removed and replaced when weighing the hives.

Once we were at the CLBS, we divided the 10 colonies into two groups: 5 fed colonies and 5 unfed colonies, with one colony of each type in each pair of colonies sharing a hive stand. The colonies were assigned to the two groups in such a way that unfed and fed colonies had, on average, equal mean amounts of drone brood, but the unfed colonies had a slightly higher mean hive weight than the fed colonies (to reduce the likelihood that the unfed colonies would starve over the next several weeks). Each colony in the fed group received 454 g of sugar each day, in the form of 770 ml of a 50% (w/w) sucrose solution. Each fed colony's food was dispensed by placing it in a quart jar with a metal lid that was perforated with small nail holes, and then inverting the jar over the opening in the inner cover of its hive. An empty hive body was placed around each feeder jar to isolate it from bees from other colonies. The emptied feeder jars were removed and replaced with filled feeder jars every morning for 27 days, from June 16 to July 12.

On the afternoon of June 26, we compared the rates of drone departure from fed and unfed colonies. To do so, we made counts of the number of drones leaving each hive in one minute. Working together, we made counts simultaneously from the two hives (one fed and one unfed) on each hive stand. We made four complete rotations among all the hives, yielding 4 counts per hive.

On July 15, we remeasured the number of frames of worker brood in each colony, using the same method as was used on June 3 (see above).

We used Student's t-tests to determine the statistical significance of the difference between fed and unfed colonies in the mean values of several variables (hive weight, frames of worker brood, drone brood area, number of adult drones ejected, number of pupal drones ejected, and number of drones departing per min). Descriptive statistics are reported as the mean ± one standard deviation.

Results

Weight gain and drone production

Figure 1 shows that the fed and unfed colonies had different patterns of weight gain over the 4-week period at Cranberry Lake. The fed colonies steadily gained weight while the unfed colonies basically maintained their weight, so that by the times of the last two weighings (July 5 and 12) the mean weight of the fed colonies was significantly greater than that of the unfed colonies (July 5: $t = 2.37$, df = 8, $P < 0.02$; July 12: $t = 3.04$, df = 8, $P < 0.01$). The fact that the unfed colonies maintained their weight (no difference in mean weight between June 14 and July 12: $t = 0.53$, df = 8, $P > 0.50$) indicates that the bees were able to find some natural sources of food, hence were not starving. We noticed too that each colony was able to collect pollen and maintain a substantial store of pollen (a rim of cells containing pollen above the brood on each frame containing brood) in its hive.

Figure 1 also shows that the fed and unfed colonies started out with essentially equal amounts of drone brood and that

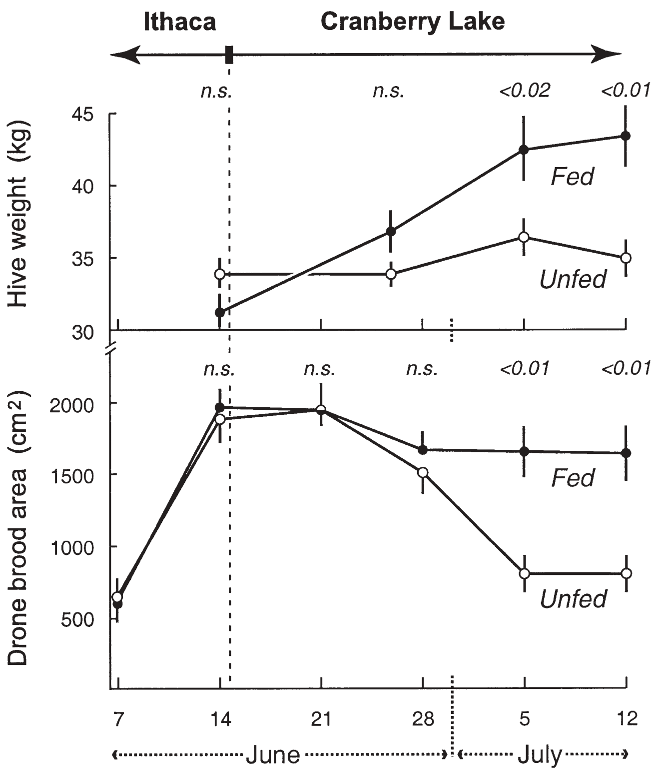

Figure 1. Patterns of change in hive weight and drone brood for 5 fed and 5 unfed colonies. Initially, the colonies were located in Ithaca, NY, a location with rich bee forage, and none of the colonies were fed. On June 15 the colonies were moved to Cranberry Lake, NY, a location with poor bee forage. Here half the colonies were fed 770 ml of 50% sucrose solution per day (454 g sucrose per day) and half the colonies were left unfed

the colonies in both groups increased greatly their investments in drone brood during the last week in Ithaca. The fed and unfed colonies also started out with equal amounts of worker brood: 4.7 ± 0.7 and 4.3 ± 0.5 frames, respectively, on June 3; $t = 1.11$, df = 8, $P > 0.25$). Once they were moved to Cranberry Lake, however, both fed and unfed colonies did not increase further their investments in drone brood. Eventually they began to lower their levels of drone brood; there was a significant reduction in mean brood area between June 14 and July 12 (fed colonies, $t = 1.80$, df = 8, $P < 0.06$; unfed colonies, $t = 4.17$, df = 8, $P < 0.01$). For the first two weeks at Cranberry Lake, the mean areas of drone brood were the same for the fed and unfed colonies, but by the end of the third week the mean area of drone brood in the unfed colonies had dropped significantly below that of the fed colonies ($t = 3.15$, df = 8, $P < 0.007$). This difference persisted through the fourth week ($t = 3.05$, df = 8, $P < 0.01$). Although the fed and unfed colonies contained markedly different amounts of the drone brood at the end of the study, they contained equal amounts of worker brood: 7.4 ± 1.8 and 8.5 ± 1.2 frames, respectively, on July 15; $t = 1.15$, df = 8, $P > 0.25$).

Drone maintenance

To see if the fed and unfed colonies differed in their levels of drone maintenance, we made daily counts of the number of adult and pupal drones in the dead bee trap on each hive. For the 4-week period at Cranberry Lake, the total numbers of adult and pupal drones collected per colony were 113 ± 93 and 15 ± 14 for the fed colonies, and 54 ± 26 and 9 ± 4 for the unfed colonies. Both means are higher for the fed than for the unfed colonies, but neither for the adult drones nor for the pupal drones is the difference between the means significant (for adults: $t = 1.37$, df = 8, $P > 0.20$; for pupae: $t = 0.78$, df = 8, $P > 0.40$). Note that for both types of colony, the mean number of dead drones per day was low: fed colonies, 4.2 adults and 0.5 pupae; unfed colonies, 2.0 adults and 0.4 pupae. Also, when the counts of dead drones collected per colony are corrected for the fact that the unfed colonies had significantly less drone brood, we see that the disparity in number of dead drones collected largely disappears: 0.072 drones collected/cm^2 of drone brood for the fed colonies, and 0.045 drones collected/cm^2 of drone brood for the unfed colonies.

Drone departures

By June 26, some 10 days after the colonies had been brought to Cranberry Lake, we had a preliminary indication of a difference in weight gain between the fed and unfed colonies, but no sign of a difference in drone production or maintenance. We wondered if the difference in energy intake between the fed and unfed colonies might be having an effect on the level of flight activity by the adult drones in the two types of colonies. The day was warm and sunny, perfect for drone flight, so we made counts of the rate of drone departure from each colony starting at 14.23 h, hence in the middle of the drone flight period. Our results are shown in Table 1. When we calculated the mean rate of drone departure for each colony (last column, Table 1), and then used these colony means to calculate a mean value for the fed colonies (11.1 ± 2.1 drones/min) and unfed colonies (4.7 ± 2.4 drones/

Table 1. Drone flight activity for the fed and unfed colonies on 26 June 2000, 14.23–15.07 h

Colony	Type	Counts of drone departures/min				
		1	2	3	4	Mean
1	Fed	13	15	17	10	13.8
2	Unfed	4	0	5	4	3.2
4	Unfed	10	4	13	7	8.5
5	Fed	10	7	8	11	9.0
6	Fed	10	14	12	11	11.8
8	Unfed	10	3	5	4	5.5
9	Fed	8	7	13	8	9.0
10	Unfed	2	3	4	6	3.8
11	Fed	15	16	6	11	12.0
12	Unfed	2	6	1	1	2.5

min), we found that the rate of drone departures was significantly higher for the fed than the unfed colonies ($t = 4.52$, $df = 8$, $P < 0.005$).

Discussion

A social insect colony, like a multicellular organism, has a life history, i.e., a pattern of birth, growth, reproduction, and death. Presumably, natural selection has shaped the main features of a colony's life cycle – how fast the colony will grow, when it will begin reproduction, how many times it will produce reproductives, how many reproductives it will produce in each bout of reproduction, and how long it will live – to produce an integrated colonial phenotype that is well „designed" for survival and reproduction. One approach to understanding the adaptive design of an individual's life history is to view the individual as having an investment policy whereby it allocates limited resources among the various physiological functions fostering its growth, survival, and reproduction. As yet, there is little systematic information on the patterns and processes of resource allocation in colonies of social insects. This study contributes to a beginning effort in this direction for honey bee colonies.

In species in which energy is a limited resource, a particularly important aspect of energy allocation is between current reproduction and parental condition (Stearns, 1989; Roff, 2001). This aspect of energy allocation has been studied in honey bee colonies by manipulating a colony's ability to invest in male reproductives (by controlling the availability of the large cells needed to rear drones) and observing the effects on the colony's energy reserve (Seeley, 2002). A strong trade-off between current reproduction (drone rearing) and parental condition (energy reserve) was found. Between mid May and late August, colonies that invested little in rearing drones built up energy reserves nearly double those of colonies that invested normally in rearing drones: 48.8 vs. 25.2 kg of honey, respectively. This finding, coupled with the fact that a colony's survival to the next reproductive season is strongly influenced by the size of its energy reserve (see Table 2 in Seeley and Visscher, 1985), makes it clear that the current reproduction vs. parental condition aspect of energy allocation is an important one in honey bee colonies. Only if this allocation is made properly will the colony survive and so have a chance of future reproduction.

What the present study shows is that a honey bee colony's policy of energy investment in current reproduction is a flexible policy. When we moved two essentially equivalent groups of colonies into an environment with few natural nectar sources, and gave the colonies in one group a positive energy budget (the fed colonies, which gained weight) and the colonies in the other group a neutral energy budget (the unfed colonies, which neither gained nor lost weight), we found that the colonies with neutral energy budgets invested less in drone production relative to the colonies with positive energy budgets. Curiously, we found no difference between the two colony types in investment in worker production; at the end of the study, the mean amounts of worker brood in the fed and unfed colonies did not differ. Evidently, when a colony experiences difficulty building the energy reserve it needs to survive to the next reproductive season, it trims its allocation of energy to reproduction, but not to growth. Such flexibility no doubt helps a colony respond adaptively to environmental heterogeneity.

Besides looking for flexibility in drone rearing, we looked for flexibility in drone maintenance. Here we obtained mixed results. On the one hand, we found no evidence that the colonies with a neutral energy budget, relative to those with a positive energy budget, invested *a great deal* less energy in maintaining their adult drones. If they had done so, then we should have seen more adult drones evicted by the unfed colonies than the fed ones, but we did not. On the other hand, we found evidence that the colonies with a neutral energy budget invested *somewhat* less energy in maintaining their adult drones. The mean rate of drone departures from the unfed colonies was markedly below that from the fed colonies. Because our comparison of the two groups of colonies was made just 11 days after the colonies were moved to Cranberry Lake, and at this point there was no detectable difference between the fed and unfed colonies in drone production or drone elimination, it is unlikely that the difference in drone departure rate arose from a difference in the number of drones per colony between fed and unfed colonies. It may be that the drones in the unfed colonies had more difficulty getting sufficient fuel to make orientation and mating flights than did the drones in the fed colonies. Free and Williams (1975) report that when they abruptly ended a colony's foraging, by placing it in a cage, the colony would evict most of its drones within a few days, but that this eviction could be prevented by feeding sugar syrup to the caged colony. Evidently, if a colony experiences a strongly negative energy budget, it can curtail quickly its allocation of energy to drone maintenance.

An attractive subject for future study is the mechanisms of social physiology which enable a colony to adjust its investment in male reproductives in relation to its energy budget. How exactly does a colony adjust its *production* of drones? Does the queen lay fewer unfertilized eggs when the workers have less success in nectar foraging? If so, then how does the queen acquire information about the colony's success in nectar foraging? Or does the queen lay the same number of unfertilized eggs regardless of the workers's foraging success, but the workers provide less care for immature drones when the nectar foraging is poor? If so, then how do the nurse bees acquire information about the colony's success in nectar foraging? And how exactly does a colony adjust its *maintenance* of drones? Do the workers simply withhold food from the drones when the nectar foraging deteriorates, or do they also attack the drones? Answers to all these questions must await further study.

Acknowledgements

This research was supported by the U.S. Department of Agriculture (Hatch grant NYC-191407). We are grateful to Dr. Stephen Teale for providing space and facilities at the Cranberry Lake Biological Station, and two anonymous reviewers for giving helpful suggestions for improving this paper.

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