

Research article

A modeling approach to swarming in honey bees (*Apis mellifera*)

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Abstract. Identifying the mechanisms of colony reproduction is essential to understanding the sociobiology of honey bees. Although several *proximate* causes leading to the initiation of queen rearing – an essential prerequisite to swarming – have been proposed, none have received unequivocal empirical support. Here we model the main proximate hypotheses (colony size, brood comb congestion, and worker age distribution) and show that all proposed swarming triggers occur as a function of the *ultimate* cause of a colony reaching replacement stability, the point at which the queen has been laying eggs at her maximal rate. We thus present a reproductive optimization model of colony swarming based on evolutionary principles. All models produce results remarkably similar both to each other and to empirically-determined swarming patterns. An examination of the fit between the individual models and swarm-preventing techniques used by beekeepers indicates that the reproductive optimization model has a relatively broad explanatory range. These results suggest that an examination into the behavioral correlates of a queen's maximum egg laying rate may provide a unified proximate mechanistic trigger leading predictably to colony fission. Generating a predictive model for this very well studied animal is the first step in producing a model of colony fission applicable to other swarm-founding eusocial animals.

Keywords: Game theory, computational model, reproductive fission.

Introduction

The theory of natural selection was built on Darwin's insight that when populations contained individuals with different heritable phenotypes, differential reproduction based on these phenotypes is sufficient to lead to evolution (Darwin, 1859). Self-sacrificing worker castes in social insect socie-

ties initially presented a conceptual problem for Darwin's theory, but Hamilton's (1964) gene's eye view of the selective benefits of seemingly altruistic behavior provided a robust explanation for the evolution of sterility. Still, reproductive behavior that occurs at the level of the group presents conceptual difficulties not experienced when examining reproduction in solitary animals. Colony-level reproduction in honey bees is one example where much confusion remains.

At any given time, a honey bee (*Apis mellifera*) colony effectively harbors only one reproductive female and the majority of her eggs develop into functionally sterile workers. A few of these eggs, however, will be treated differently and will develop into new queens. Before these rising queens mature, mate and lay eggs of their own, the old queen leaves the colony and takes with her approximately 75% of its adult bees (Fig. 1). This behavior – reproductive swarming – is the colony's method of reproducing (reviewed in Winston, 1987). Accordingly, an understanding of swarming is crucial to a complete understanding of the life cycle and behavior of the honeybee (Oster and Wilson, 1978).

Although fascinating from behavioral and evolutionary perspectives, swarming is also of interest for agricultural purposes. Bees are kept, not only for their production of honey, but also for their crucial role in pollination (Southwick and Southwick, 1992). Indeed, the value to the US economy of pollination alone has been estimated at over \$14 billion per year (Morse and Calderone, 2000). Since 'bee production', 'honey-storing' and 'normal foraging' are all interrupted by swarming, understanding and being able to manipulate swarming behavior can have a direct and critical impact on agricultural practices (Wenning, 2000). Beekeepers have traditionally used a variety of techniques to inhibit swarming, none of which have been found unambiguously reliable (Caron, 2000; Wenning, 2000; Winston et al., 1980).

A natural question follows: "What causes honey bees to swarm?" Because normal swarming will not occur without first initiating the process of queen rearing, characteristics leading to queen rearing are likely to be causal factors leading

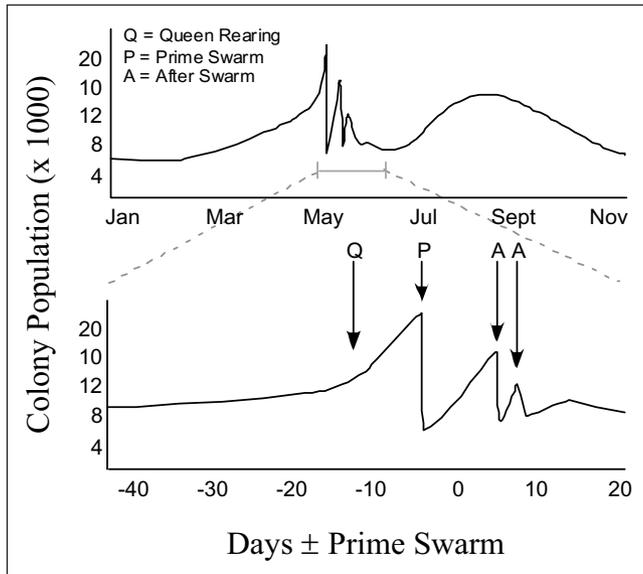


Figure 1. Time specific colony size and swarming patterns (Fig. 11.1 in Winston [1987]). In the month represented in the graph by days -40 to -10 , the colony grows by $\sim 3,000$ bees. In the days represented by days -10 to day 0, the colony grows by $\sim 10,000$ bees. Since the average life expectancy of a worker over the growing season is 31 days (Winston, 1987), over the course of a month, all of the workers must be replaced. In order for a colony to grow by 3,000 bees (from 9,000 to 12,000), the queen must have laid (starting 21 days in advance) 9,000 eggs to replace the original population and 3,000 additional eggs in order to increase the colony size. As such, the queen must have laid 12,000 eggs in the course of 31 days. This indicates that her laying rate is approximately 400 eggs per day. Similarly, in order for the colony to grow from 12,000 to 22,000 bees over a period of 10 days, she must have laid as many eggs as would replace approximately $1/3$ of the original 12,000 bees, in addition to the 10,000 necessary to increase the colony size. This indicates that the queen is laying approximately 1,400 eggs per day during this period. These numbers imply a sharp increase in egg laying rate at a particular point in the growing season.

to swarming (Winston, 1987). Many different hypotheses have been proposed to explain the initiation of queen rearing and, hence, swarming. The following list, while not exhaustive, forms a representative sample of such hypotheses. (For a more complete overview, see Winston, 1987.)

Colony size: The active worker population reaches a particular size and/or density threshold during a time of accelerated population growth and this triggers queen rearing.

Brood nest congestion: As the queen continues to lay an increasing number of eggs over time, the number of empty cells in the brood comb decreases. The greater numbers of eggs necessitate an increase in the number of adult workers caring for the brood. This increased density of adults on the brood comb, coupled with the decreased density of empty cells into which the queen can lay her eggs, triggers queen rearing.

Worker age distribution: At the beginning of the growing season, the age distribution of a colony is greatly skewed towards older (≥ 24 days old) workers. Gradually, as the older workers die and increasing numbers of eggs are laid,

develop into adults, and eclose to take their place, the proportion of younger (≤ 7 days old) workers increases. Once this proportion of younger workers reaches a particular threshold this triggers queen rearing.

Reduced transmission of queen pheromones: Queen honey bees produce pheromones that have been shown to inhibit queen rearing in workers (Winston et al., 1990). These pheromones are transmitted both directly from queen to worker and between workers via ‘messenger bees’ (Seeley, 1979). As the colony grows in size and becomes increasingly congested, the queen and her messengers either come into direct contact with each worker less frequently, or else maintain their contact rate with a progressively smaller proportion of the worker population, thereby weakening the effective ‘dose’ of pheromone each is able to deliver. This reduced dispersal of the queen’s pheromones triggers queen rearing.

Winston (1987) has combined these mechanisms into an elegant flow diagram of queen rearing and subsequent swarming, and suggests that the multifactorial nature of the process accounts for the lack of unequivocal support for any single mechanistic hypothesis. Indeed, the pheromone transmission hypothesis is itself a multi-factor hypothesis, as reduced transmission is a function of colony size and brood comb congestion.

An alternative explanation for the inability to support a single mechanism is that instead of being causal triggers, the hypothesized mechanisms are simultaneous artifacts (i.e. correlates) of the actual mechanistic cause of swarming. That is, there may be a single underlying mechanism coincident with the above-mentioned factors. Even if *what* causes a colony to swarm is unclear, *why* swarming happens at a particular time in the development of a colony seems clear: colonies swarm when characteristics indicate a high likelihood of reaching the evolutionary objective of successful reproduction.

The exact developmental stage of a colony is a function of many factors, thus for any given stage of development there will be quantifiable states of food storage, nest building, worker development, and population size. These states are properties of the colony’s developmental stage and, for colonies preparing to swarm, may be inherent in the conditions associated with queen rearing without necessarily causing queen rearing. Accordingly, we might expect that each factor (e.g., large colony size, brood comb congestion, etc.) would be consistently observed in conjunction with queen rearing and swarm departure, but that experiments manipulating these factors would not necessarily affect swarming behavior because the factors in question would also be the result of the stage of colony development.

This paper presents a mathematical model of an *ultimate* hypothesis for swarming in temperate species *A. mellifera* (that is, for honey bees with a defined swarming season). In so doing we also present mathematical expressions for previously published *proximate* hypotheses of swarming behavior. It is important to note that ultimate and proximate hypotheses are not mutually exclusive (Sherman, 1988). Accordingly, our approach will not isolate ‘the’ proximate

mechanism(s) leading to swarms, though it does suggest a few previously unexamined possibilities. We call our hypothesis the Reproductive Optimization hypothesis. In generating this hypothesis, we have assumed that honey bee colonies are selected to maximize fitness and that the optimum fitness level is a function of queen quality, specifically her egg laying potential.

While not necessarily the case in all social insects, in honey bees the rate of colony growth is primarily determined by two factors: the number of workers available to support the colony and the maximum number of eggs an established queen can lay in a given period of time. Thus, there may be instances when there are enough workers to support a greater number of eggs than the queen can produce. The colony would then reach a steady state, neither growing nor shrinking, not because the workforce could not support growth, but because the queen would be unable to produce additional eggs. Once this point of 'replacement stability' is reached, the production and support of another queen is the only way to satisfy the evolutionary goal of increasing the rate of production of bees related to the colony.

Colonies approaching replacement stability will necessarily present many of the observed phenomena proposed as swarm triggering mechanisms. Specifically, a colony approaching replacement stability immediately prior to swarming will: firstly, reach its greatest numbers, thus coinciding with the Colony Size hypothesis; secondly, contain relatively few unused cells in the brood comb, thus coinciding with the Brood Nest Congestion hypothesis; thirdly, have reared progressively larger numbers of workers which skews colony demography in favor of younger bees, thus coinciding with the Worker Age Distribution hypothesis; and finally, contain younger brood-tending workers in the now congested brood comb, which decreases the mobility of messenger nurses, thus coinciding with the Reduced Transmission of Queen Pheromones hypothesis.

By making a few simplifying assumptions (Appendix 1) and constructing mathematical models, we are able to carefully quantify the implications of each of the hypotheses. In this way, we can compare the implications of our ultimate hypothesis with those of each of the proximate hypotheses and determine if these latter hypotheses are based on characteristics of colonies approaching replacement stability. Accordingly, we can simultaneously examine our hypothesis with published data used in generating the proximate hypotheses, and examine the proximate hypotheses in relation to each other. A number of papers have modeled the possibility of reduced pheromone transmission in congested hives (e.g. Baird and Seeley, 1983; Naumann et al., 1991; Watmough, 1997), and empirical studies have established the inhibitory effect of queen pheromone on queen rearing (Winston et al., 1990), however, no study has examined the actual transmission of pheromones in swarming colonies. We have not produced a model for this hypothesis because pheromone transmission is assumed to be a direct function of the other proposed mechanisms, and thus is not hypothesized to happen in the absence of the mechanisms we are examining.

Methods/Model

Any mathematical model is a simplification of the system it models. Its goal is to accurately represent the aspects of the system that most greatly affect the outcome in question. In our study of swarming, we have chosen to focus on the ergonomics and energetics of the hive as a reproductive system. Use of this modeling method has provided insight into the behaviors of social insects (e.g., Oster and Wilson, 1978). Given this foundation, we then alter the factor behind the decision to initiate queen rearing and, therefore, swarming. This leads to a unique model for each proposed hypothesis. We then examine the effects of these different mechanisms on both the timing of, and colony structure associated with, the production of swarms. In order to be sure that no other factors confound the results of our models, parameter values are held constant across all models, as are equations governing colony growth. Only the factor causing swarming is altered.

Intuitively, the models of all of the hypotheses function in the following way: at the start of the growing season, a colony is assumed to have an 'average' population size, F (estimated in Winston [1987]). During each day of the growing season, i , the net gain in energy, U , produced by the adult workers in the parent colony is used to rear new workers. While there are certainly other energy-requiring tasks performed by workers during the growing season (e.g. honey storage), we have chosen to represent all effort in terms of energy benefits and costs focusing on the rearing of new workers. Other tasks can be thought of as incorporated into the gross costs without being included in the net gain. The growth rate is therefore determined by the number of individuals which can be supported by the produced excess, E_i , unless the excess is able to support more individuals than the queen's maximal daily laying rate, p . In this case, the number of new eggs is capped at that maximum. It is assumed that each individual receives the same amount of attention (energy), N , even those which are assumed to die before developing into an adult workers. (We have assumed a uniform, combined egg and larval mortality rate of 11%, however, since this was held constant across all models, it had no effect on the comparative results.) The parent colony queen is restricted from laying eggs for ten days prior to swarm departure (Gilley and Tarpy, 2005; Winston, 1987) and the newly risen queen is similarly restricted for ten days subsequent to the departure of the primary swarm (Gilley and Tarpy, 2005). The mathematical formulation, variable relations and equations comprising each iteration (day) of this model are listed in Table 1.

The differences among the models for each of the separate hypotheses lies in the trigger of the decision to swarm. This trigger, A_i , is adjusted for each hypothesis and incorporated accordingly into the model (see Table 2). For purposes of establishing the values once the colony had achieved replacement stability, an additional version of the model, not corresponding to any of the hypotheses, is prohibited from swarming.

With the models defined in this way, we are able to vary the starting size of the parent colony, the foraging success of the workers and the maximum reproductive rates of the queens and compare the resultant predictions of when swarming will occur throughout the growing season (see Table 3 for variable values and appendix 1 for model assumptions). We have chosen to limit the number of possible swarms produced to two for both computational simplicity and ease of comparison with the swarm departure curve given in Winston (1987) (see Fig. 1).

Results

Each model independently produced primary swarms between days 69 and 74 of the growing season (Table 4). Both the Colony Size model and the Worker Age Distribution model produced identical results, matching each other in all pertinent aspects (Figs. 2a–c). The Reproductive Optimization model differed from the Colony Size and Worker Age

Table 1. The mathematical formulation of the model described above in Section 2.0. Each variable is defined below. Table 3 lists the values used for each parameter.

Description	Variable/Parameter	Definition
The number of eggs laid on day i	E_i	$\max \left(0, \min \left(\frac{M_C}{N}, qp \right) \right)$ if $\{i < I_{S_1} - 10$ or $I_{S_1} + 10 < i < I_{S_2} + 10$ or $i > I_{S_2} + 10\}$ OR 0 if $\{I_{S_1} - 10 \leq i \leq I_{S_1} + 10$ or $I_{S_2} - 10 \leq i \leq I_{S_2}\}$
The day of the growing season when the k^{th} swarm leaves the parent colony	I_{S_k}	(see Table 3)
The amount of energy needed to produce and feed one egg until eclosion	N	(see Table 3)
The maximum egg laying rate of the queen of the parent colony	p	(see Table 3)
The rate of egg survival to eclosion	q	(see Table 3)
The average net amount of energy produced by all of the colony workers on day $i-1$	M_C	$(U) * C_{i-1}$
The net amount of energy one worker is able to produce for the colony per day (on average)	U	(see Table 3)
The average size of a colony coming out of overwintering at the beginning of the growing season	F	(see Table 3)
The size of the parent colony on day i	C_i	F if $\{i \leq 21\}$ OR $[C_{i-1} + E_{i-21} - (F/30)]$ if $\{21 < i \leq 30\}$ OR $[C_{i-1} + E_{i-21} - (7F/10)]$ if $\{i = 31\}$ OR X_i if $\{32 \leq i \leq 180\}$
Determination of colony size on day i between days 32 and 180 of the growing season	X_i	$[(C_{i-1} + E_{i-21} - E_{i-51}) * (L_{S_1})]$ if $\{A_i = 10 \ \& \ H_i = 1 \ \& \ I_{S_1} = i\}$ OR $[C_{i-1} + E_{i-21} - (E_{i-51} * L_{S_1})]$ if $\{A_i < 10 \ \& \ H_i = 1 \ \& \ I_{S_1} \geq i-10\}$ OR $[(C_{i-1} + E_{i-21} - E_{i-51}) * (L_{S_1}) * (L_{S_2})]$ if $\{A_i = 10 \ \& \ H_i = 2 \ \& \ i < I_{S_1} + 31\}$ OR $[(C_{i-1} + E_{i-21} - E_{i-51}) * (L_{S_1})]$ if $\{A_i = 10 \ \& \ H_i = 2 \ \& \ i \geq I_{S_1} + 31\}$ OR $[(C_{i-1} + E_{i-21} - E_{i-51}) * (L_{S_1} - (L_{S_1} * L_{S_2}))]$ if $\{H_i = 2 \ \& \ i > I_{S_1} + 31 \ \& \ i \leq I_{S_1} + 10\}$ OR $[(C_{i-1} + E_{i-21} - (E_{i-51} * L_{S_1} * L_{S_2}))]$ if $\{H_i = 2 \ \& \ i < I_{S_1} + 51 \ \& \ I_{S_2} < i \leq I_{S_2} + 31\}$ OR $[(C_{i-1} + E_{i-21} - (E_{i-51}))]$ if $\{\& \ i > +51 \ \& \ i < +31\}$ OR $[C_{i-1} + E_{i-21} - E_{i-51}]$ if $\{(A_i = 0 \ \& \ H_i = 0 \ \& \ i < I_{S_1})$ or $(A_i < 10 \ \& \ H_i = 1 \ \& \ i > I_{S_1} + 31)$ or $(H_i = 2 \ \& \ i \geq I_{S_2} + 31)\}$
The percentage of the parent colony expected to leave with the k^{th} swarm	S_k	(see Table 3)
The percentage of the parent company expected to stay when the k^{th} swarm leaves	L_{S_k}	$(1 - S_k)$
The decision variable triggering the decision to swarm	A_i	(For the definitions associated with each model, for each hypothesis, see Table 2.)
The number of swarms which have left the parent colony by day i	H_i	–
The threshold colony size sufficient to trigger swarming in the Colony Size hypothesis model	T	(see Table 3)

Table 2. The definitions of the decision variable A_i used as the trigger for the decision to swarm in each of the models.

Hypothesis	Description	Definition for A_i
Reproductive Optimization	Swarming is triggered when the workers can support more eggs than the queen can lay.	$0 \text{ if } \left\{ \left(\frac{M_{C_{i-21}}}{N} < qp \right) \text{ or } (A_{i-1} > 9) \right\}$ <p>OR</p> $1 \text{ if } \left\{ \left(\frac{M_{C_{i-21}}}{N} \geq qp \right) \right\}$ <p>OR</p> $[A_{i-1} + 1] \text{ if } \{A_{i-1} \leq 9\}$
Colony Size	Swarming is triggered if the size of the colony exceeds the threshold T	$0 \text{ if } \{(C_i < T) \text{ or } (A_{i-1} > 9)\}$ <p>OR</p> $1 \text{ if } \{(C_i \geq T) \text{ or } (H_i = 1 \ \& \ i = I_{S_i} + 1)\}$ <p>OR</p> $[A_{i-1} + 1] \text{ if } \{A_{i-1} \leq 9\}$
Worker Age Distribution	Swarming is triggered if the workers which have eclosed during the past 7 days comprise more than one third of the active worker population	$0 \text{ if } \left\{ (H_i = 0 \ \& \ \frac{\sum_{m=i-30}^{i-22} E_m}{C_i} < \frac{1}{3}) \text{ or } (A_{i-1} > 9) \right\}$ <p>OR</p> $1 \text{ if } \left\{ (H_i = 0 \ \& \ i > 43 \ \& \ \frac{\sum_{m=i-30}^{i-22} E_m}{C_i} \geq \frac{1}{3}) \text{ or } (H_i = 1 \ \& \ i = I_{S_i} + 1) \right\}$ <p>OR</p> $[A_{i-1} + 1] \text{ if } \{A_{i-1} \leq 9\}$
Brood Comb Congestion	Swarming is triggered if the combined number of eggs and larvae in the brood comb is greater than 17,000	$0 \text{ if } \left\{ (H_i = 0 \ \& \ \sum_{m=i-21}^i E_m < 17,000) \text{ or } (A_{i-1} > 9) \right\}$ <p>OR</p> $1 \text{ if } \left\{ (H_i = 0 \ \& \ \sum_{m=i-21}^i E_m \geq 17,000) \text{ or } (H_i = 1 \ \& \ i = I_{S_i} + 1) \right\}$ <p>OR</p> $[A_{i-1} + 1] \text{ if } \{A_{i-1} \leq 9\}$
No Swarming Allowed	Regardless of colony conditions, swarming is never triggered	0

Distribution models by at most 3% of the stabilization value in any one proposed triggering mechanism at the appropriate time to cause queen rearing to begin (Table 4). The Brood Nest Congestion model produced swarming three days earlier than any of the other models, but produced the same shape curve as the other swarming models (Figs. 2a–c). The model which was not allowed to swarm stabilized in all values by the hundredth day of the growing season. (Note that the colony size cannot stabilize until after the maximal egg clutches have been hatching for as long as the average life span of a worker over the growing season. This means that

the colony size will automatically stabilize 31 days after the first maximal egg clutch is laid.)

Regardless of the mechanism used, each model failed to produce values sufficient to trigger the swarming until it had also produced values sufficient (within 6% of stabilization value) to trigger swarming by any/all of the other proposed mechanisms. Each of the models also produced a colony size prior to and directly after swarming which closely fit the expected colony size from the swarm departure curve given in Winston (1987) (see Fig. 1). (Since our models were not allowed to produce multiple afterswarms, our results cannot be

Table 3. The estimated values used in each of the models. These values were held constant over all of the models. While they are necessary in order to be able to compare the results of each model to the reported swarm departure curve given in Winston 1987 (see Fig. 1), they do not influence the comparison of the results of the models to each other.

Parameter	Value	Reference
U	0.01 mg honey	Winston (1987)*
N	0.151 mg honey	Winston (1987)
S ₁	70 %	Winston (1987)*
S ₂	55 %	Winston (1987)*
q	89 %	Assumed
p	900 eggs	Winston (1987)*
F	5000 bees	Winston (1987)*
T [†]	16,000 bees	Winston (1987)*
Duration of worker pre-adult life	21 days	Winston (1987)
Average worker life expectancy	31 days	Winston (1987)

* Numbers inferred from Fig. 1.

† In the Colony Size Hypothesis Model only.

compared to those in Winston's curve past the point of the first afterswarm.)

Discussion

Model Results

All proposed hypotheses generate models that predict colony population and swarming patterns that closely match reported numbers (Winston, 1987; Fig. 1). In fact, all of the models, regardless of the trigger mechanism, predict nearly identical curves describing colony size (Fig. 2a), timing of the onset of swarming during the growing season (Table 4), brood comb congestion (Fig. 2b), worker age distribution (Fig. 2c) and, based on these similarities, possibly queen pheromone transmission. While it is possible that more than one mechanism is at work to trigger queen rearing, the individual models, without any interaction, are sufficient to produce colony sizes and swarm timing similar to those previously observed (Winston, 1987; Fig. 1).

These results suggest that all of these phenomena are observed before swarming, not because they are individually the specific causes (or are operating in conjunction as a unified cause), but because they are all properties of hives nearing the same point in colony development which itself prerequisite to the initiation of swarming. Though they have historically been treated as separate and individual hypotheses (Winston, 1987), the hypothesized mechanisms are actually interdependent consequences of a hive nearing 'replacement stability', i.e., the point at which colony size can no longer be increased. The results from our models imply not only that we would expect all factors to be reliable precursors of queen rearing and subsequent swarm departure, but that they cannot occur independently of each other.

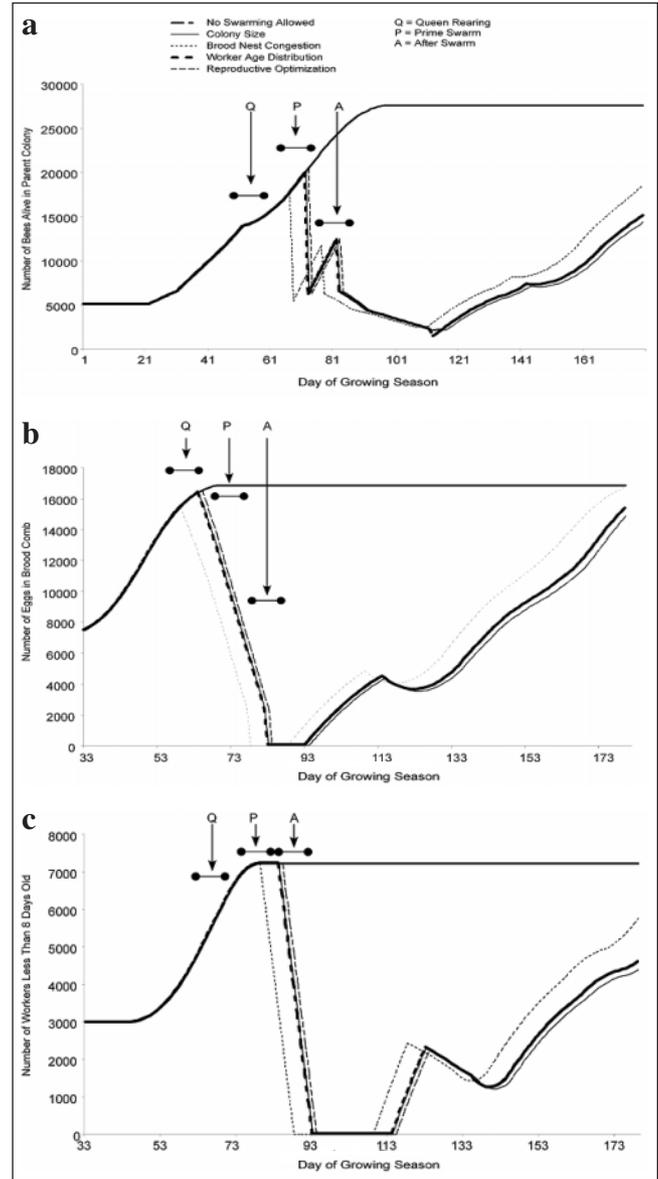


Figure 2. The timing of swarm production, the increase in colony size, the skew of the worker age distribution, and the increase in brood congestion were similar for all hypotheses, regardless of the trigger mechanism modeled. The barbells indicate the range of time corresponding to queen rearing (Q), primary swarm departure (P) and secondary swarm departure (A) over all models. **a:** At any time during the growing season, the number of bees in the parent colony produced by each swarming model closely track each other. Only the model which artificially disallowed swarming exceeded any of the other population sizes by more than 5 % of the maximum stable population size. **b:** The colony size, worker age distribution and reproductive optimization models produced identical numbers of eggs in the brood comb prior to, during and after swarming within one day of each other. For each of these models, the swarm departed within five days of reaching replacement stability. The brood nest congestion model produced a swarm slightly earlier than any other model and ultimately allowed the brood to reach maximal levels by the end of the growing season. **c:** All of the models reached a stable maximum of young workers within the twenty one days egg development time from swarm departure (all but the brood nest congestion model coincided to within a day of each other). While this is exactly the timing we would expect from the reproductive optimization hypothesis, every model produced the same results.

Table 4. Results of the individual models.

Model	Day of First Swarm Departure	Total Number of Eggs 10 Days Before First Swarm Departure	Number of Workers <8 First Days Old 10 Days Before Swarm Departure	Total Size of Colony 10 Days Before First Swarm Departure
No Swarming Allowed*	NA	16,821	7,209	27,530
Colony Size	73	16,221 (96%)	4,849 (67%)	16,110 (59%)
Brood Nest Congestion†	69	15,391 (91%)	4,126 (57%)	14,743 (54%)
Worker Age Distribution	73	16,221 (96%)	4,849 (67%)	16,110 (59%)
Reproductive Optimization	74	16,373 (97%)	5,046 (70%)	16,449 (60%)

* All values for the No Swarming Allowed model are stabilization values.

† Values for Brood Nest Congestion Model may be low due to possible elimination of "primary need" limiting factor.

(%) Represent the percentage of the stabilization value.

Implications

While our model cannot reject the previously hypothesized proximate mechanisms, it does suggest an additional set of mechanisms that have yet to be explored. For example, because our reproductive optimization hypothesis is tied directly to the queen's egg laying rate, workers may respond to a colony-wide leveling off of brood related tasks by initiating queen rearing. Alternatively, workers may be able to assess the queen's egg laying rate directly. This may involve either sufficient concentrations of egg marking pheromones (c.f. Martin et al., 2004). Such preparation may involve vibration signaling behavior: workers have been observed to vibrate queens with increasing frequency leading up to primary swarm departure (Schneider, pers. comm.). It is possible that the frequency of this signal functions as part of the swarming trigger mechanism. While these remain hypotheses, our approach may be suitable to help explain some of the inconsistent results generated when testing the mechanistic hypotheses.

Table 5 outlines a few methods used by beekeepers to minimize swarming. While no method has been shown to be completely successful (Winston et al., 1980; Winston, 1987), examining the individual hypotheses with respect to these methods is informative. For example, according to the Queen Pheromone Transmission hypothesis, one might predict that the confines of an observation hive are too severe to inhibit transmission of pheromones, especially when volatiles influence worker behavior (e.g. Moritz and Southwick, 1986). Small observation hives have been used for a great deal of swarm-based research (Gilley and Tarpy, 2005), however, so this hypothesis appears insufficient as a complete explanation. Similarly, the Age Distribution hypothesis makes the prediction that shrinking the worker population while holding other factors constant should lead to more swarming because the result would necessarily be a younger mean age as new individuals eclosed. It is common practice among beekeepers, however, to remove workers to minimize the chance of swarms (Winston et al., 1980). Removal of brood comb is another method used by beekeepers to minimize swarms (Winston et al., 1980), but the Colony Size hypothesis would predict this to be ineffective and the Brood Nest Congestion hypothesis may, depending on the form of comb used as a

replacement, predict that this would increase swarming behavior.

The Reproductive Optimization hypothesis predicts that swarming behavior will be reduced with the removal of workers and of brood comb because, with the former, fewer workers will be available to rear offspring, thus limiting the queen's egg output. With the latter, fewer workers will eclose to help rear offspring. Our hypothesis also suggests that when external constraints are removed (e.g., by increasing the physical size of the colony), swarming will still occur when the queen's egg laying rate reaches its maximum. When severe constraints are added (e.g., when in an observation hive), the queen's maximum egg laying rate will be artificially reduced, and thus swarming should occur. Alternatively, when the size of the hive is expanded to unnatural proportions by supplementation with empty comb, one might predict that the queen would appear relatively weak to a colony.

Supersedure – the rejection of a queen and production of another – can, in addition to swarming, be viewed as result of assessing the strength of a queen. This additional phenomenon can now be understood within the context of our model. For example, a colony would be able to support all of the possible eggs from a queen with a low maximum laying rate very early in the growing season. This would imply stability at an unusually low population level. For a colony to survive the departure of a swarm, initially it must rely on the eggs left by the old queen to rebuild its workforce. If those clutches were small, the remaining colony (at ~25% strength) might not be able to grow large enough to survive the upcoming winter. If the queen's maximum reproductive rate is too low, deposing her in favor of a new queen would greatly increase the colony's ability to survive the depletion suffered subsequent to swarm departure. This hypothesis may help explain why colonies are likely to supersede when the queen is damaged, diseased, or laying too few eggs (Winston, 1987).

Life-History

It is not our intention to suggest that the reproductive optimization hypothesis invariably explains swarming behavior, but we do suggest that our model is a reasonably good fit

with published data. All models, however, are insufficient to explain all aspects of the colony cycle. All of the models, for instance, produce results, regardless of their trigger mechanism, sufficient to trigger swarming during the end of August (although, by capping the allowable number of swarms produced at 2, we have artificially prevented this from occurring). As this is generally not observed, it is reasonable to assume that there is a point (i.e., a failsafe) in the growing season past which swarming will not occur because it would leave the parent colony too depleted and the swarm too small for either to successfully overwinter. After the failsafe is reached, we would expect the frequency of swarms to be very low regardless of the trigger.

In addition, while our model uses the size of the workforce as a direct proxy of the number of newly laid eggs a colony can support, it is clear that queen's laying rate does not increase gradually but rather increases dramatically prior to the primary swarm (Fig. 1). This rapid increase in egg laying may indicate a 'primary need' limiting factor: a threshold which must be passed before the queen and colony dedicate themselves to rearing as many eggs as possible. One such hypothesized threshold is based on forage availability and is often called the resource abundance hypothesis for swarming (Winston, 1987). One likely candidate is pollen, as provision of pollen has been shown to result in brood production during periods when production would normally halt (Standifer et al., 1977).

Viewing swarming as a game theoretic optimization of colony level reproduction presents us with a means of empirical verification: providing varying levels of energy resources to similarly sized populations, with similarly productive queens, should significantly alter the timing of swarming. High energy availability should cause swarming much earlier in a season than would low energy resources, regardless of the trigger mechanism being used. By understanding the underlying causality, we can carefully construct predictions for particular manipulations of colony structure (see Table 5).

Previous Research

Mathematical models of reproductive fission in honey bees have already been employed to explore the implications of the Colony Size Hypothesis (McClelland and Rowland, 1986). To determine the timing and duration of the swarming period under this single hypothesis, McClelland and Rowland applied a deterministic model that allowed the colony to swarm once it had achieved sufficient population size, given particular constraints on the timing of swarm production. By altering the initial population size, the interval prior to swarming during which the queen was restricted from egg-laying, the proportion of the adult population departing with the primary swarm, and the number of larvae supported by a single adult worker, they were able to determine that the Colony Size Hypothesis proposed trigger mechanism is most sensitive to the egg laying rate of the queen. While this model lends no insight into the ultimate cause of why the Colony Size Hypothesis would be evolutionarily successful, it provides valuable insight into how robust this mechanism is to each of the contributing factors of colony growth.

Mathematical models have also been employed in order to study the hypothesis that reproductive fission in colonies of social insects occurs so as to increase colony-level reproductive fitness (Franks, 1985). Franks provided a model for fission in colonies of army ants (*Eciton burchelli*), predicting that colonies should undergo fission as soon as the combined rate of the growth of the two resultant daughter colonies would equal that of the original parent colony, thereby minimizing the time between generations and allowing maximal reproduction over time. In army ants, this is a convenient metric to assess since the resultant daughter colonies are of equal size and the egg laying rates of the new queens are assumed to be constant over time (i.e. relatively unlimited by foraging success), and equivalent both to each other's and to that of their parent queen.

This system differs from that of the honey bee in a number of ways. (1) In honey bees, different queens can have extremely different egg-laying potentials (ant queens were assumed to have equivalent laying potentials in Franks'

Table 5. Expected results of different trigger mechanism hypotheses on the various experimental swarm-preventing manipulations. Our assumed starting condition for the hive is that swarming is imminent, just prior to the production of queen cells (e.g., the queen has reached maximal egg laying rate, the colony has reached a certain number of workers, etc.). Swarm-preventing manipulations include: Small worker population (the removal of workers), low brood comb density (the removal of brood comb), and large & small hive sizes (an increase or decrease in physical hive size, respectively). Yes: manipulation is expected to affect swarming; No: manipulation is not predicted to affect swarming; arrows indicate increase or decrease in swarming.

	Small Worker Population	Low Brood Comb Density	Large Hive Size	Small Hive Size
Reproductive Optimization	Yes (↓)	Yes (↓)	No [†]	Yes (↑)
Brood Nest Congestion	No	Yes (↑↓)*	Yes (↓)	Yes (↑)
Worker Age Distribution	Yes (↑)	No	No	No
Queen Pheromone[‡]	Yes (↑↓)	Yes (↑↓)	No	Yes (↑↓)
Colony Size	Yes (↓)	No	No	No

* Depending on treatment

† See text

‡ Recall that the Queen Pheromone hypothesis is actually a combination of the Brood Nest Congestion and Colony Size hypotheses and predictions depend on whether queens or messenger bees are responsible for pheromone transmission

model). (2) Fission in honey bee colonies produces two colonies of unequal size which greatly influences subsequent success and survival. (3) The honey bee colonies resulting from fission experience unequal constraints: the daughter colony inherits not only the nest, but also developing eggs which will provide additional workers over time, thus deferring the potential attrition of the workforce.

Differences between honey bees and army ants make the application of Franks' daughter-colony growth rate model to honey bees difficult. The differences between systems, however, can be thought of as altered constraints on colony growth within the framework of our game theoretic model. Indeed, our framework can be extended to any social insect system that displays reproductive fissioning. By applying the underlying concept of constraint-limited growth rate eventually leading to colony size stabilization to Franks' model, we see that, in fact, he also predicts that the growth potential of daughter colonies will equal the growth rate of the parent colony only as the parent colony itself nears replacement stability (see Fig. 9 in Franks [1985]). This result is exactly as predicted by the reproductive optimization hypothesis.

Conclusion

Identifying the mechanisms of colony reproduction is essential to understanding the sociobiology of honey bees. By modeling the prevailing mechanistic hypotheses for queen rearing and swarming, we show that all proposed triggers occur as a function of a colony reaching replacement stability. An examination of techniques used by beekeepers to inhibit swarming, displays a reasonably good fit with the reproductive optimization model. As such, our results suggest that an examination into the behavioral correlates of a queen's maximum egg laying rate may provide the as yet unknown proximate mechanistic trigger leading predictably to colony swarming. Importantly, while our model presents an attempt to understand this fundamental element in the life cycle of honey bees, our examination of the army ant example indicates that our concept and methods can easily be generalized to other systems.

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Appendix 1: Model Assumptions

1. All bees live exactly as long as their average life expectancy (31 days: Winston [1987]).
2. Egg survival is independent from food resource limitations other than those resulting directly from a limited workforce.
3. A queen's maximum egg laying rate is uniform and constant across all times for each queen.
4. A growing season is 180 days long.
5. Drones have no effect on colony growth.
6. A pre-existing colony will produce at most two swarms during a growing season.

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